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NEW WORLD NECTAR-FEEDING BATS: BIOLOGY,
MORPHOLOGY AND CRANIOMETRIC APPROACH TO
SYSTEMATICS

by

ERNST-HERMANN SOLMSEN

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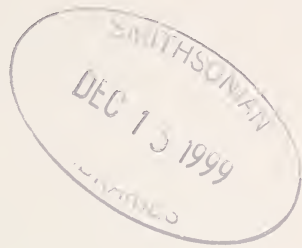
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INTRODUCTION

With more than 900 species, the Chiroptera represent the most comprehensive mammalian order next to the rodents. By developing physical ability for continuous flight bats succeeded in exploring habitats almost without vertebrate competitors - the nocturnal airspace. Their morphological adaptations are just as consistent; having specialized their anatomy in flight and a hanging resting position, most bats are hardly capable of quadrupedal locomotion, apart from crawling over short distances.

General body shape hardly varies within the Chiroptera - presumably due to strict requirements for free flight. Differences are delicate and restricted to body size, wing shape, development of the urotagium and tail length. However, the chiropteran head is one of the most striking characters in specific determination. Due to echolocation many microchiropterans show an oddity of complex structures on ears and often also nose which aid in directed emission and perception of sound.

Having successfully conquered the nocturnal skies, the primarily insectivorous Chiroptera developed a variety of new diet preferences - carnivory (*Megaderma*, *Vampyrum*, *Phyllostomus*, *Trachops*), piscivory (*Pisonyx*, *Noctilio*) and even - unique among the mammalia - sanguivory (*Desmodus*, *Diaemus*, *Diphylla*). Besides, many species also take vegetable food: frugivorous and even few nectarivorous species prevail among the Megachiroptera (Pteropodidae), but also the Microchiroptera developed a variety of fruit and flower-feeding genera within the Phyllostomidae.

These various diet preferences within the Microchiroptera have their morphological expression primarily in the shape of the head and in the dentition. Thus, skull morphology of bats developed some remarkable diversity within the mammalia.

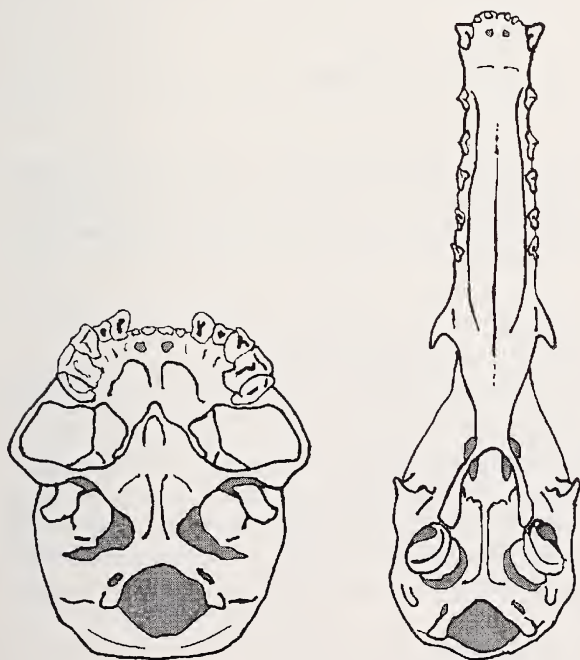


Fig.1: Skull shape depending on diet specialization within the Phyllostomatidae (*Centurio senex* = fruit eater, *Choeronycteris harrisoni* = blossom feeder, adapted from Koopman 1987)

In this respect, some members of the phyllostomid family achieved a striking diversity, with the highly specialized flower bats representing an extreme (fig.1).

Especially the Glossophaginae succeeded in extensive specialization (prolongation of the rostrum; long tongue with bristle-like papillae, weak and delicate teeth). The systematic integration of all long-nosed Phyllostomids into a single monophyletic subfamily is still discussed controversially. As the main characters used to define glossophagine bats are derived characters influenced by function, they could well have developed independently within the phyllostomids.

For more than 25 years, several approaches have been made to this problem (tab.1) and various different systematic relationships of single genera were proposed from time to time.

Table 2: Studies on the system of New World nectarfeeding bats

| | |
|--|---|
| - morphological examinations teeth, dentition gastrointestinal system tongue, hyoid musculature female sex apparatus cerebral anatomy | (Phillips 1971) (Forman 1971, 1979; Rouk & Glass 1970) (Wille 1954; Greenbaum & Pillios 1974; Griffiths 1982) (Smith & Hood 1982) (McDaniel 1976) |
| - cytological examinations chromosomal analysis hematology | (Baker et al. 1967; Patton & Gardner 1971; Stock 1975; Baker & Bass 1979; Haiduk & Baker 1982) (Valdivieso & Tamsit 1971) |
| - immunological studies serum proteins serum proteins | (Baker et al. 1981) (Gerber & Leone 1971) |

Classification of *Brachyphylla* as an essentially basic form within its own subfamily Brachyphyllinae remained undisputed (Baker et al. 1979) as well as everyone agreed to summarize the genera *Erophylla* and *Phyllonycteris* within the Phyllonycterinae (Flower vampires), a subfamily closely related to the Brachyphyllinae (Silva Taboada & Pine 1969).

Contrary conclusions primarily concern the systematic position of the genera or subfamilies having been summarized so far as Glossophaginae.

Some really revolutionary improvement was achieved by the works of Griffith published 1982. Analyzing the tongue and hyoid morphology and their musculature, respectively, he was the first to separate three genera (*Lionycteris*, *Lonchophylla* and *Platalina*) from the Glossophaginae s.str., summarizing them within their own subfamily Lonchophyllinae.

These results led to a lively discussion between different research groups in the United States (Haiduk & Baker 1982; Warner 1983; Hood & Smith 1982; Griffiths 1983; Smith & Hood 1984). The point of this discussion is: do the New World nectarivorous bats represent a monophyletic group, or did the glossophagine bats develop twice, independently from each other?

Even within nectar feeders, among all morphological structures, the skull undoubtedly was the main structure to undergo (possibly different) adaptations to intake of food. They are

numerous and sometimes extreme. According to the bounty of differently specialized species modifications in skull structures vary with degree of specialization on nectar feeding. Adaptations affect the visceral skull as well as the neurocranium. Dentition, mandibular and palatal bones show modifications of remarkable extent. Even the braincase changes its bony processus as a consequence in reduced masticating musculature.

So, subsequently, the skull morphology of the New World nectarivores and related phyllostomid genera will be examined comparatively.

The aim is to understand and to describe the principles of skull construction in nectar feeding phyllostomatids as an adaptation to nectar feeding. Allometrical comparison of cranio-metric data will result in some evidence on suprageneric relationships of the genera.

As an introduction to this subject, chapter 2 will give an overview on systematics, distribution and ecology of New World flower bats, mostly compiled from available literature.

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At the Zoologic Museum of the University of Hamburg I was supported by Mrs. U. Frerichs who prepared the skull drawings of the genera which had only been accessible abroad and thus sometimes were represented by insufficient photographs.

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Last, but not least I like to thank Prof. Dr. Harald Schliemann for introducing me to the world of these fascinating mammals.

ON THE SYSTEMATICS, DISTRIBUTION AND ECOLOGY OF NEW WORLD FLOWER BATS

Taxonomic Position

All neotropic flower bats belong to the New World phyllostomids (Phyllostomatidae):

Order Chiroptera

Suborder Microchiroptera

Superfamily Phyllostomatoidea

Family Phyllostomatidae / (Phyllostomidae)

Subfamilies:

Lonchophyllinae

Brachyphyllinae

Phyllonycterinae

Glossophaginae

Phyllostominae

Stenoderminae

Caroliinae

Currently, the Phyllostomatidae are divided into seven subfamilies of which four subfamilies contain 38 predominantly nectarivorous species in 15 genera:

Subfamily Lonchophyllinae Griffiths, 1982

Genus *Lionycteris* Thomas, 1913

L. spurrelli Thomas, 1913

Genus *Lonchophylla* Thomas, 1903

L. thomasi Allen, 1904

L. dekeyseri Taddei, Vizotto & Sazima, 1983

L. mordax Thomas, 1903 with subspecies

L. robusta Miller, 1912

L. handleyi Hill, 1980

L. bokermanni Sazima, Vizotto & Taddei, 1978

L. hesperia Allen, 1908

Genus *Platalina* Thomas, 1928

P. genovensium Thomas, 1928

Subfamily Brachyphyllinae Gray, 1866

Genus *Brachyphylla* Gray, 1834

B. nana Miller, 1902 (= *B. pumila* Miller, 1918)

B. cavernarum ssp. Gray, 1834 with subspecies

Subfamily Phyllonycterinae Miller, 1907

Genus *Erophylla* Miller, 1906

E. sezekorni (Gundlach, 1861) with subspecies

E. bombifrons (Miller, 1899) with subspecies

E. b. santacristobalensis: Hispaniola

E. b. bombifrons: Puerto Rico

Genus *Phyllonycteris* Gundlach, 1861

Subgenus *Phyllonycteris* Gundlach, 1861

Ph. (Ph.) poeyi Gundlach, 1861 with subspecies

Subgenus *Reithronycteris* Miller, 1898

Ph. (R.) aphylla (Miller, 1898)

Subfamily Glossophaginae Bonaparte, 1845

Genus *Glossophaga* Geoffroy St.Hilaire, 1818

G. soricina (Pallas, 1766) with subspecies

G. s. handleyi (= *G. s. leachii*): North America

G. s. mutica: Island population Tres Marias Is.

G. s. antillarum: Jamaica I.

G. s. valens: South America, Ecuador, Peru

G. s. soricina: South America (east of Andes)

G. commissarisi Gardner, 1962 with subspecies

G. longirostris Miller, 1898 with subspecies

G. leachii (Gray, 1844) (= *G. morenoi* Martinez & Villa, 1938; =*G. alticola* Davis, 1944)

G. mexicana Webster & Jones, 1980

Genus *Monophyllus* Leach, 1821

M. redmani Leach, 1821 with subspecies

M. plethodon Miller, 1900 with subspecies

Genus *Leptonycteris* Lydekker, 1891

L. nivalis (Saussure, 1860)

L. yerbabuenae Martinez & Villa-R., 1940 (= *L. sanborni* Hoffmeister, 1957)

L. curasoe Miller, 1900 with subspecies

Genus *Lichonycteris* Thomas, 1895

L. obscura Thomas, 1895 (= *L. degener* Miller, 1931)

Genus *Anoura* Gray, 1838

A. caudifer (Geoffroy St.Hilaire, 1818)

A. cultrata Handley, 1960 (= *A. brevirostrum* Carter, 1968; = *A. werckleae* Starrett, 1969)

A. geoffroyi Gray, 1838 with subspecies

A. latidens Handley, 1984

Genus *Hylonycteris* Thomas, 1903

H. underwoodi Thomas, 1903 with subspecies

Genus *Scleronycteris* Thomas, 1912

- S. ega* Thomas, 1912
- Genus *Choeroniscus* Thomas, 1928
 - Ch. godmani* (Thomas, 1903)
 - Ch. intermedius* (Allen & Chapman, 1893)
 - Ch. minor* (Peters, 1869) (= *C. inca* Thomas, 1912)
 - Ch. periosus* Handley, 1966 with subspecies
- Genus *Choeronycteris* Tschudi, 1844
- Subgenus *Choeronycteris* Tschudi, 1844
 - Ch. (Ch.) mexicana* Tschudi, 1844
- Subgenus *Musonycteris* Schaldach & McLaughlin, 1960
 - Ch. (M.) harrisoni* (Schaldach & McLaughlin, 1960)

Geographic Distribution

The 13 genera of the subfamilies Glossophaginae and Lonchophyllinae are distributed throughout the subtropical and tropical areas of the New World. Two further, very closely related (Silva-Taboada & Pine 1969) subfamilies of the Phyllostomatidae, the Brachyphyllinae and Phyllonycterinae, also comprising nectarivorous species, are restricted to the islands of the Caribbean. Some genera, like *Glossophaga soricina* or *Anoura geoffroyi* are widespread with distributional ranges as far from southern United States down to southern Peru. Others have an extremely restricted distribution: the Banana bat (*Choeronycteris harrisoni*) which probably shows the highest adaptation to nectar feeding was not discovered before 1960, and only very few specimens were subsequently captured near the same locality from Central Mexico.

Data on the geographic distribution predominantly refer to the locality of the collected material; subsequently individual taxa are given in a detailed list of all currently known distribution areas:

Subfamily Lonchophyllinae

Lionycteris

L. spurrelli: E Panama to E Peru and Brazilian Amazon region, west of the Andes, however, not south of Colombia

Lonchophylla

L. thomasi: Eastern Panama to E Peru and Amazon region of Brazil, but west of the Andes to the south not beyond Ecuador

L. dekeyseri: E Brazil

L. mordax: Costa Rica to W Ecuador (*L. m. concava*) and E Brazil (*L. m. mordax*)

L. robusta: Nicaragua to N Peru; east of W Venezuela

L. handleyi: Ecuador and Peru (east of the Andes)

L. bokermanni: SE Brazil

L. hesperia: Arid regions in SW Ecuador and NW Peru

Platalina

P. genovensium: restricted to arid regions of Western Peru

Subfamily Brachyphyllinae

Brachyphylla

- B. nana*: Cuba, Island Hispaniola, Cayman Islands and southern Bahama Islands (fossil from Jamaica)
B. cavernarum: Puerto Rico, Virgin Islands except island St. Croix (*B. c. intermedia*), St. Croix, Anguilla south to St. Vincent (*B. c. cavernarum*) and Barbados Islands (*B. c. minor*)

Subfamily Phyllonycterinae

Erophylla

- E. sezekorni*: N and central Bahama Islands (*E. s. planifrons*), SE Bahama Islands (*E. s. mariguanensis*), Cuba, Cayman Islands (*E. s. sezekorni*) and Jamaica (*E. s. syops*)
E. bombifrons: Island Hispaniola (*E. b. santacristobalensis*), Puerto Rico (*E. b. bombifrons*)

Phyllonycteris: Cuba, Hispaniola und Jamaica (rezent), fossil from Puerto Rico

Ph. poeyi: Cuba (*Ph. p. poeyi*), island Hispaniola (*Ph. p. obtusa*)

Ph. aphylla: Jamaica

Subfamily Glossophaginae

Glossophaga

- G. soricina*: North American Mainland (*G. s. handleyi* = *leachii*); Tres Marias Islands (*G. s. mutica*); Jamaica (*G. s. antillarum*); South American mainland, Ecuador, Peru (*G. s. valens*); South America east of the Andes (*G. s. soricina*)
G. commissarisi: Southern Mexico (*G. c. commissarisi*), northwestern Mexico (*G. c. hespera*)
G. longirostris: NW Ecuador, N Colombia, NW Venezuela (*G. l. longirostris*); northern South America, Caribbean (*G. l. elongata*); E Colombia to Trinidad I. (*G. l. major*); S Venezuela and Guayanas (*G. l. campestris*); Central Colombia (*G. l. reclusa*); Tobago and Grenada Islands to St. Vincent I. (*G. l. rostrata*)
G. leachii: Nicaragua
G. mexicana: Southern Mexico east of Oaxaca and W Chiapas (*G. m. mexicana*); western Oaxaca to Michoacan (*G. m. brevirostris*)

Monophyllus

- M. redmani*: Jamaica (*M. r. redmani*); Cuba, island Hispaniola, southern Bahama Islands (*M. r. clinedaphus*); Puerto Rico (*M. r. portoricensis*)
M. plethodon: Barbados Island (*M. p. plethodon*); Puerto Rico (subfossil) (*M. p. frater*); Lesser Antilles from Anguilla south to St. Vincent (*M. p. luciae*).

Leptonycteris

L. nivalis: Texas to Guatemala

L. yerbabuenae: Arizona, NE Mexico to El Salvador

L. curasoae: South American mainland, Isla Margarita and Aruba Islands (*L. c. tarlosti*) Curacao and Bonaire (*L. c. curasoae*)

Anoura

A. caudifer: Restricted to tropical South America east of the Andes, Colombia to the Amazon delta, NW Argentina and SE Brazil

A. cultrata: Costa Rica to N Venezuela and Bolivia; however, not beyond west of the Andes

A. geoffroyi: Tropical Mexico to W Ecuador (*A. g. lasiopyga*), central Colombia to central Bolivia (*A. g. peruana*) Venezuela, Guayana, Trinidad, Grenada Islands, E Bolivia to eastern Brazil (*A. g. geoffroyi*)

A. latidens: N Venezuela to E Peru

Hylonycteris

H. underwoodi: Western Mexico from Jalisco to Oaxaca (*H. u. minor*); Veracruz to Panama, incl. Belize (*H. u. underwoodi*).

Scleronycteris

S. ega: Southern Venezuela, northwestern Brazil (Amazon region)

Choeroniscus

C. godmani: W Mexico and northern fringe of South America to Surinam

C. intermedius: Trinidad I., Guyana, Surinam, N Brazil and Peru (east of the Andes)

C. minor: South American tropics from W Ecuador to the Amazon delta, north to E Venezuela and south to NW Bolivia

C. periosus: W Colombia (*C. p. periosus*), northwestern Venezuela (*C. p. ponsi*)

Choeronycteris

C. mexicana: SW USA to Honduras incl. Tres Marias Islands

C. harrisoni: SW Mexico (Colima, Guerrero u. Michoacan)

Habitat, roosting behaviour, migration

The ecology of bats is predominantly determined by two elements: finding food on one hand and on the other - just as compelling - finding suitable day shelter. Thus, any locality of collected material will only reveal half of the occupied habitat. An insight to the ecological demands of a chiropteran species will only be gained by long-term field observations or by comparative observations of captive animals in their roost and during foraging. But the capturing data of most specimens allows - at least tentatively - assessment to the habitat of the species. Accordingly, the members of some genera are restricted to tropical rainforest (*Choeroniscus*, *Hylonycteris*, *Lichonycteris*), while others occur almost everywhere (*Anoura*, *Glossophaga*, *Lonchophylla*). Some genera (*Leptonycteris*, *Platalina* and *Choeronycteris*) are adapted to arid areas, where they predominantly feed on cactus flowers.

These highly adapted flower visitors depend on pollen as a protein source all around the year. Unless they cover larger distances they can only get it in the highly constant milieu of the neotropical rainforest. This ecological request is mainly due to the fact that hovering flight requires a relative high amount of energy in food intake (v. Helversen & Reyer 1984). One strategy to succeed with limited sources is outrunning intraspecific competition - this will only work in low population densities and within large distribution areas (e.g. Amazon rain forest). Here, most nectarivorous bats inhabit territories in small family groups all the year round (*Choeroniscus*, Koepcke 1987).

There are, however, areas, where seasonal peaks of food supply determine the amount of food available to the bats, requiring a quite different strategy. Thus *Leptonycteris*, though highly specialized on blossom food, lives in large colonies - all the host plants of their arid habitats usually bloom simultaneously, providing a rich food supply over a short time. In need of constant food supply, the animals are forced to visit their host species currently flowering within various areas, and often cover considerable distances (Humphrey & Bonaccorso 1979). Furthermore, climate changes require long migrations, as the bats are

incapable of surviving by means of prolonged lethargy phases. Onset of the rainy season with the climate getting cooler sets off migration in *Leptonycteris* (Easterla 1973). During summer, *L. nivalis* is found in the higher levels of Big Bend National Park, Texas, and several areas of Northern Mexico; and in winter they go further south, passing down at least to Jalisco and Morelos (Barbour & Davis 1969; Kunz 1982).

Where the supply of night-flowering plants does not support a minimum of individuals required to sustain genetic diversity, these habitats will be compliant to less specialized genera who also include quite a lot of small insects in their diet (*Glossophaga*, *Anoura* and *Lonchophylla*). Correspondingly, most of them have more extensive distribution areas.

Habitat data on single taxa:

Lionycteris: Most specimens of *L. spurrelli* Handley (1976) recorded in Venezuela were captured in humid forest, roosting in caves and rocky crevices during the day. In Peru, Tuttle (1970) captured two bats at the edge of indigenous villages, one of them amongst flowering Cashew trees.

Lonchophylla: Spends the day in hollow trees, sometimes in caves. In Venezuela, Handley (1976) collected most of his *L. robusta* and *L. thomasi* in humid forested areas. Detailed information on *L. thomasi* from the Peruvian rain forest was given by Koepcke (1987). From six specimens, three were captured in open riverine woodland, two in a tall cassava field and one at a river bank. Several months she observed these bats in their day shelters beneath embankments and among the roots of hollow trees. Though they sometimes moved to another roost, the species altogether proved sedentary during the mating season.

Platalina: There are no ecological data on *Platalina genovensium* yet.

Brachyphylla: These bats prefer caves, though there are some records from buildings and one from a well (Novak & Paradiso 1983). They live in small groups (Beatty 1944) or in large colonies (5000 - 10,000 individuals). Their day shelters are not always in the dark (entrance areas of caves, well shafts, dense foliage). As observations in captive specimens revealed that they do prefer the darkest area of their cages, staying within lighter areas may be accepted as a temporary behaviour (Swanepoel & Genoways 1983).

Erophylla: Buden (1976) recorded *E. sezekorni* not only from the deeper, darker cave areas but also from the lighter surroundings of the entrance. Koopman et al. (1957), however, collected their specimens on several islands of the Bahamas exclusively in the deeper cave areas.

Phyllonycteris: Roosts in caves during the day (Novak & Paradiso 1983).

Glossophaga: *G. soricina* exploits a variety of different roosts - natural hideouts like caves, hollow trees and crevices, but also artificial hiding-places: drainage pipes, deserted mines, cellars, roof framework or undersides of bridges (Tuttle 1976; Webster 1982). According to this wide range of roost selection they show a considerable compliance to other bat species: there are more than 30 other species which are known sometimes to share the same roost (Webster et al. 1984). The strongest coincidence is found with *Carollia perspicillata*: In Peru, more than 60% of all known day shelters have been recorded for both genera (Graham 1988). Apparently, the members of both taxa even share the same locations within a shelter forming mixed clusters - probably an evidence of mutual benefit by means of socialization, such as less effort in thermoregulation and water budget. According to Koepcke (1987), *G. soricina* prefers lighter vegetation or densely covered cultivated land. One of the bats she observed flew between the dwelling

houses, another amidst a tall corn field. Various *Glossophaga* were recorded from a banana plantation at a woodside and next to a river.

Monophyllus: *M. redmani* prefer humid caves, where they usually live in colonies of considerable size. Sexes apart from each other the individuals cling to the walls, the ceilings and chimneys in dense clusters (Homan & Jones 1975). *M. plethodon* is exclusively known from netted individuals. As there is also one record of a dead specimen in front of a cave entrance in Dominica Island (Schwartz & Jones 1967) these bats presumably accept caves as day shelters.

Leptonycteris: *L. nivalis* is a colonial cave dweller which is also found in adits, deserted buildings and hollow trees. Such caves are characterized by a musk-like scent resembling that of *Tadarida brasiliensis* (Barbour & Davis 1969). The size of the colonies may exceed 10 000 individuals: Easterla (1972) reported a population density of 1615 bats per square meter!

Lichonycteris: All records are from dense rain forest areas; up to now no data on roost selection.

Anoura: In Venezuela, Handley (1976) found *Anoura* predominantly in humid and woodland areas, often at high altitude. They spend the day in crevices and caves.

A. cultrata reportedly inhabits higher levels (mountainous forests from 220 m to 2600 m) (Tamsitt & Nagorsen 1982). Most often the localities are in humid rain forest areas where the animals are caught with nets along rivers or streams or at the edge of clearings or villages. The specimens I caught myself in Ecuador spent the day in a very humid cave (San Antonio de Pichincha, height 2300 m above sea level).

A. caudifer has been reported by Koepcke (1987) from the Amazon area of Peru from cultured areas next to woodland, but she did not detect any roost sites. - One specimen collected in 1983 at Rio Cuyabeno, Ecuador, was also caught with a net at sunset at a riverine woodside next to a banana plantation. Their preferred roost sites include tree hollows, caves, drainage pipes, sewers and buildings. Up to 13 individuals were recorded at one single location. In Manaus, Reis (1981) detected three individuals in a fallen hollow log in the company of *Micronycteris megalotis*.

Hylonycteris: Phillips & Jones (1971) collected *H. underwoodi* in dense woodland of Jalisco, Mexico. Some small groups of two and eight individuals were reported by Laval (1977) under a wooden bridge and a hollow tree. This species, however, also accepts caves and tunnels as roost sites (Allen 1942), but apparently in small groups of very few individuals only. In Guatemala, one female was caught together with two specimens of different species *Glossophaga* and one *Lichonycteris obscura* next to a night-blooming tree. Currently, nothing is known about their socialization in the roost site.

Scleronycteris: One of the three known specimens Handley (1976) netted in Tamatama, Rio Orinoco, T.F. Amazonas, Venezuela, at a riverine jungle clearing.

Choeroniscus: Several individuals of *C. intermedius* have been reported by Koepcke (1987) from the Amazon basin of Peru roosting in small groups or in pairs under logs or in hollow trees in riverine areas. Three of them were found separately among the roots of fallen trees, one pair beneath the bark of a rotten log. All individuals were 50 - 70 cm above the floor and occupied their gloomy roost sites for several months. Three *C. intermedius* she caught at the edge of a primary forest, one of them flying above a low field and another at a dead water of Rio Lullapchis. One specimen of *C. minor*, captured at Rio Cuyabeno in Ecuador 1980, was also found at a river bank (Patzelt pers. comm.).

There is also one Venezuelan report on eight specimens hanging beneath a log which had fallen across a river (Sanborn 1954).

Choeronycteris: *C. mexicana* is known from various habitats, from arid brier to tropical secondary forest and mixed oak wood (Arroyo-Cabrales et al. 1987). As day shelters they prefer caves and deserted adits, usually clinging themselves at dim recesses next to the entrance. So, they accept even very small caves. There is some controversy about whether they congregate with other species: whereas Goodwin (1946) regarded *C. mexicana* as a mostly solitary species merely moving about, there have been later reports on various Vespertilionidae and *Tadarida*, also *Glossophaga*, sharing their roost sites with these bats. They occupy both caves and artificial shelters. Davis & Russell (1954) found a group of *C. mexicana* hanging beneath a tree. The individuals cling separately 2 - 5 cm apart from each other, usually holding grip with only one foot and thus capable of observing intruders by rotating their body up to 360 degrees. *C. mexicana* is an extremely alert, easily startled species, which will rather leave the roost immediately than move to darker sites (Barbour & Davis 1969).

Activity Patterns

Brown (1968) pointed out how activity patterns depend on diet: correspondingly, insectivorous species are most active in the early evening, whereas frugivorous and piscivorous bats show almost equal activity patterns all over the night. In the sanguivorous Desmodontidae, the activity pattern is mainly determined by darkness, as these bats are most active at complete darkness. Nectar feeding bats leave their roosts soon after sunset heading for their host plants according to certain patterns, so their activity pattern sometimes may be bimodal. They are, however, certainly active during the first half of the night.

Detailed information is available for only few species.

There are some observations on the food intake of *Lonchophylla thomasi* from east Peru by Koepcke (1987) showing that these bats leave their roosts at complete darkness not before 18.25 or 18.35. One specimen covered with pollen was caught around 9 p.m.; at least one activity phase occurs during the first night hours.

As reported by Swanepoel & Genoways (1983), *Brachyphylla cavernarum* leave their day shelter some time after nightfall, at least one hour after sunset and some 20 minutes later than *Artibeus*. First, all individuals of a colony fly out synchronously, finishing their activity almost as simultaneously within the very last minutes before sunrise.

Activity patterns of *Glossophaga soricina* were studied by Erkert & Kracht (1978), revealing that this species is influenced by a quite inflexible circadian system which synchronizes with light and is induced by sunset, with a free periodic length of just 23.4 to 25 hours merely adapting to external stimuli. In eastern Peru, Koepcke (1987) captured foraging *G. soricina* shortly before midnight, and they were observed at banana blossoms in the early morning as well. In a similar way Sazima & Sazima (1978) reported an accumulation of foraging bats between 1.20 and 4.00 a.m., with activity maxima in the evening and during the last night hours (La Val 1970; Bonaccorso 1979).

According to Fleming et al. (1972), Sazima & Sazima (1978), Bonaccorso (1979) and Koepcke (1987), spatial distribution of food supply determines the flight routes in *G. soricina*. Depending on the pollen suppliers available, the species heads for higher or

lower vegetation levels, approaching individual plants in a trap-lining way keeping a certain sequence and sometimes covering considerable distances. On their way the bats regularly visit night shelters for about half an hour. *G. soricina* approaches flowering plants both individually and in groups, the size of the latter depending on the number of open blossoms per night and tree.

As reported by Barbour & Davis (1969), *Leptonycteris nivalis* leave their roost comparatively late in the evening, but detailed information on their activity is still to come.

Chronological shifts in activity rhythms within the same habitat were reported by Koepcke (1987) in Panguana (Peru) in three sympatric nectar feeding genera: *Lonchophylla thomasi* always flew into the nets before 9 p.m., *Choeroniscus intermedius* between 8 and 11 p.m. and *Anoura caudifer* never before midnight.

Feeding biology / Feeding ecology

Chiropteran adaptations to nectari- and pollenivory

The Glossophaginae represent small to mid-sized Phyllostomatidae with a reduced dentition, a distinctly elongated nose and a widely protrusible tongue - all adaptations to a feeding specialization on nectar and soft fruit. In ecological respect they represent nocturnal equivalents of hummingbirds, and their development may partially have been influenced by similar parallel evolutionary constraints. This is shown in many similarities (weight limit, ability of hovering, elongated tongue, prolongation of the rostral skull). They usually feed during hovering, but sometimes the bats will go down onto the blossom, thereby impairing further development of the fruit with the claws.

Body size and weight

In contrast to frugivorous Phyllostomids which often grow quite large, the highly specialized nectar feeding bats range at the lower level of body size and weight (cf. tab.2). This is partly explained by ecological aspects of the flowers, as size and structure of "bat blossoms" must be sufficiently resistant to bear the weight of approaching and often even landing bats. On the other hand, body size of these animals will be essentially limited by Table 2: Body length and weight of blossom-feeding Microchiroptera (adapted from Dobat & Peikert 1985)

| | body length (mm) | weight (g) |
|---------------------------------|---------------------|------------|
| <i>Vampyrum spectrum</i> | 125-135 | 145-190 |
| <i>Phyllostomus hastatus</i> | 100-130 | 52,2-101,1 |
| <i>Phyllostomus discolor</i> | 75-91 | 22,2-40,0 |
| <i>Choeronycteris harrisoni</i> | 80-89 | ca. 25 |
| <i>Choeronycteris mexicana</i> | 60-86 | 10-20 |
| <i>Leptonycteris nivalis</i> | 76-78 | 18-30 |
| <i>Glossophaga soricina</i> | 48-84 | 5,4-12,7 |
| <i>Anoura geoffroyi</i> | 60 | 11,3-17,7 |
| <i>Choeroniscus godmani</i> | 53-58 | 7,6 |
| <i>Lichonycteris obscura</i> | 46-55 | 7,1-8,1 |

the energy balance which can be achieved. The more a bat specializes on limited plant food species, the more its body size will be restricted by comparatively expensive approaches to single flowers.

Body shape

Wing aspect ratio; phalanges

As in other flying vertebrates, the geometry of wing surface related to body weight gives some insight into flight conditions and flight demands of bats, respectively (Smith & Starrett 1979). Thus, relative length of the wing bones participating in flight activity will be determined by aerophysical demands rather than by systematic relationship - large or stocky species have longer 2. phalanges in their 3rd digit. So, differentiation corresponding to relative length of the phalanges in digit III gives evidence of wing shape: the longer the metacarpals, the narrower the wing (in fast, tenacious flyers). On the other hand, bats with comparatively stout metacarpals have broader wings (slow, astute flyers, foliage gleaners).

Early as 1943, Sanborn classified the Glossophaginae into two groups, referring to relative length of metacarpals and phalanges:

- 1) First phalanx III longer than 1/3 of metacarpal length III and second phalanx of 3rd finger shorter than 1,5 times the length of first phalanx III: *Glossophaga*, *Lichonycteris*, *Scleronycteris*, *Choeroniscus*, *Hylonycteris*, *Choeronycteris*, *Platalina*
- 2) First phalanx III shorter than 1/3 of metacarpal length III and
 - a) Second phalanx III shorter than 1,5 times the length of first phalanx III: *Lonchophylla* and *Leptonycteris* (meaning the smaller species within each genus), *Monophyllus*
 - b) Second phalanx III longer than 1,5 times the length of first phalanx III: *Lionycteris*, *Anoura*, *Lonchophylla* and *Leptonycteris* (meaning the large species within each genus).

All these results correspond to what we currently know on bat ecology. The genera mentioned first with comparatively short metacarpals usually represent highly specialized nectar feeders requiring astuteness rather than velocity when patrolling among the blossoms. Though *Glossophaga* feeds a good deal on insects, these bats presumably capture them on the substrate, not in the air. In case of *Leptonycteris*, predominantly a hovering nectar feeder, the unusual long-winged profile may not be explained by its feeding ecology alone. Here, the "wing geometry of fast and long-range flight" may have been of evolutionary significance for seasonal migrations (Sahley et al. 1995). *Anoura* reportedly takes a large proportion of insects in their diet (Gardner 1977); it is, however, questionable whether the relatively elongated wings could be explained as a device for capturing insects in flight (obviously, the morphology of the uropatagial region seems to oppose this opinion, see below) and requires further observation.

Uropatagium, tail

The degree of tail membrane development and the presence or absence of a bony tail may be interpreted as an ecological adaptation leading to selective advantages both in foraging and roosting behaviour. Within the primarily insectivorous microchiroptera, a well developed uropatagium with a long bony tail and long cartilaginous calcars is regarded as a plesiomorph condition. Within the Phyllostomatidae there are numerous variations, including a lacking tail, calcar or uropatagium (*Sturnira*, *Anoura*), various intermediate stages and extreme conditions as a short uropatagium combined with a long, projecting

tail (*Phyllonycteris*, *Monophyllus*) or an extensive tail membrane with the tail remaining very short or lacking at all (*Stenoderminae*, *Choeroniscus*). Generally, the frugivores tend to develop a reduced uropatagium, as they need to climb about on their host plants, especially when the bats even have their roosts among the branchwork or the foliage.

Most nectar feeding bats possess reduced or entirely lacking tails (*Leptonycteris*, *Anoura*). The degree of development does, however, not necessarily correspond to the degree of specialization on nectar feeding (cf. figures of interfemoral membranes in 'Results: morphology of the species examined'), but might also have been influenced by some additional ecological demands.

Pelage

An overview on adaptations of hair structure to pollen intake was given by Howell & Hodgkin (1976): even visible to the naked eye, living specimens have their nape hairs standing up like the bristles of a bottle brush rather than recumbent as in other bats.

Further differences are revealed in their fine structure: whereas many Chiroptera usually have a smooth hair shaft under the microscope, pollinating bats possess scales standing up from the shaft, thus facilitating pollen fixing in the pelage.

Fixing pollen is not only advantageous for the host plants to be pollinated - as nectar is predominantly an energy supplier, the intake of pollen serves as an essential and sometimes exclusive protein source. According to Howell (1974), analysis of stomach contents in bats having been caught at their feeding plants always revealed nectar exclusively in the stomach (and pollen only in the fur). Very probably the bats take up pollen afterwards, grooming in their roosts. Howell (1974) described that the bats ingest the pollen combed from the fur with the claws by constantly licking their feet. This behaviour is also supported by faeces analysis (Harris 1959), showing that in no case there was any anther material in the faeces of nectar feeders. Using the fur for pollen transport, the animals keep full stomach capacity for their "fuel" (the nectar). Considering the narrow limits of their energy balance, this may be a pre-condition for efficient exploitation of these resources (v. Helversen & Reyer 1984).

Dobat & Peikert (1985:110) point to the fact that the chiropteran fur generally is well suited for pollen transport, thus doubting the significance of Glossophagine fine hair structure in allowing pollen transfer. Comparable conditions to those described by Howell & Hodgkin (1976) were found independently in some non-pollenivorous bats. Thus, the fine structure of the hair shaft enlarging the surface may be determined by different ecological demands; this characteristic seems to occur widely among bats. Obviously, it seems impossible to prove any anthophile specializations in pollinating bats compared with insectivorous species, the scales on the hair shaft which are arranged like keratinized cones - as found in the pelage of all nectar feeders - certainly represent ideal devices for embedding and fixing pollen grains.

Digestive tract

Tongue

The long, tapering, very protrusible and highly mobile tongue represents the characteristic feature of specialized nectar feeding bats. Its tip is covered with brush-like papillae directed backward and thus enabling efficient nectar intake (Griffiths 1978). The protractility of the tongue is incredible - *Glossophaga* can extend its tongue up to three times the snout length. In the extremely long-nosed banana bat *Choeronycteris harrisoni* the extended tongue is up to 76mm long - corresponding body length of 80mm (v. Helversen 1993).

Early authors supposed the long tongue to be folded in an s-shape within the closed mouth (Moller 1932). Next, the tongue was disproved to be inserted within a dermal pouch as in woodpeckers or Pholidota. In fact, the tongue, when not in use, shortens to an extent that it fits into the mouth cavity. Later on, anatomical studies revealed an extremely complex morphology of the tongue musculature.

The M. genioglossus is broadened into an extrinsic tongue muscle, the M. sternohyoideus is integrated into the tongue as a retractive muscle ("In functional terms, it could be called Sternoglossus" Wille 1954; "tunnel insertion" in Griffiths 1983) and considerably lengthened - its origin at the sternum being shifted back from the manubrium to the base of the xiphoid process. Simultaneously, the insertion of the M. stylohyoideus at the tongue is shifted from ventral to lateral, thus enabling to support the M. sternohyoideus when retracting the tongue.

In *Glossophaga*, the tongue is passed through by one comparatively enormous central artery (Lonchophyllinae: two arteries) and two lateral large veins (Griffiths 1978). The latter are covered by muscle bundles which contract and press the stemmed flow of blood up to the tongue tip thus elongating and stiffening the tongue additionally (vasohydraulic tongue). All the time the entire tongue remains entirely flexible and can be bent in all directions. Furthermore, it reacts with a reflex on contact with sugar, thereby moving into nectar droplets without need of visual control.

Thus, the nectar supply is exploited within very short time. It is, anyway, still unknown how the rapid in- and efflux of the blood necessary for the high frequent licking movements - 12 movements per second (v. Helversen & v. Helversen 1975) is achieved.

Dorsally and laterally the tongue is covered with papillae, while its underside is completely smooth. A detailed description of various papillae was given by Griffiths (1982). Essentially, effective nectar intake is achieved by means of the hair papillae (Papillae filiformes) of the tongue situated at the anterior third and laterally (brush-like tongue). Aided by specialized lateral (Lonchophyllinae) or median (Glossophaginae) grooves, these structures retain considerable amounts of fluid which is set free by compression of the tongue at the palate during retraction. Nevertheless, the detailed process and the coordination of tongue motoricity and swallowing are not yet sufficiently known.

Esophagus

All chiropterans have a quite narrow esophagus, as they usually chew up their food thoroughly before swallowing. This is the same in nectar feeders which take in fluid food or very small particles. Compared to insect-eating chiropterans, the esophagus epithelium is much thinner in nectar feeding bats (Dobat & Peikert 1985) and not keratinized as in pure insect-eaters.

Stomach

The stomach of blossom bats is designed to take large quantities of fluid within a rather short time. According to Howell (1979), *Leptonycteris* will absorb 4g - corresponding to 22% of its body weight - within just 20 minutes. Interestingly, the muscle layer of the stomach is very thin. In macroscopical respect there is a conspicuously oversized blind sack and an enlarged pylorus area, both features contributing to the necessary volume capacity. Furthermore, the low proportion of pepsinogen producing cells within the fundus glands of the mucosa (Rouk & Glass 1970, Forman 1971) correlates with the diet being comparatively poor in proteins.

Intestines

Generally, Chiroptera have quite short intestines, presumably a concession to their flight ability. Thus, indigestible bits are expelled after a surprisingly short time. Among bats, the frugivorous species have the longest intestines, whereas the latter are very short in insect-eaters and flower bats - probably due to their diet containing more energy. This may also explain their astuteness in flight.

Adaptations in host plants to Chiropterophily

Size and Constitution

Despite of their low weight - even in terms of chiroptera - nectar feeding bats represent heavyweights compared to other pollinators. This influenced both the structure of the blossoms and the entire constitution of chiropterophilous plants. Though the plants belong to completely different taxa they do share some common features: according to Baker (1961), plants which are supposed to be pollinated by bats must be strong and thus are usually tree-shaped. So, we find the following form types in order of frequency (Dobat & Peikert 1985):

1. Trees (e.g. *Ceiba*, *Crescentia*, *Parkia*)
2. Shrubs (e.g. *Symbolanthus*)
3. Pillar cacti (e.g. *Carnegia*)
4. Lianas (e.g. *Mucuna*)
5. Epiphytes (e.g. *Capanea*, *Markea*, *Trienaea*, *Vriesea*)
6. Herbaceous plants (e.g. *Agave*, *Musa*)
7. Herbs (e.g. *Lisianthus*)

Undoubtedly, most of them are woody, tree-shaped plants. Though the existence of quite low, ground growing chiropterophilous herbaceous plants and herbs seems to be incompatible with these physical demands, Baker's view as cited is nevertheless supported in two respects: first, these plants are quite rare, and second, they tend to gigantism. All in common their blossoms are shifted as high as possible, thus facilitating orientation for the bats approaching them and at the same time reducing access for unspecific and thus less efficient nectar consumers.

Blossom shape

There is an enormous variety in adaptations which cannot be discussed in detail here (review in Dobat & Peikert 1985). It is, however, interesting how some chiropterophil plants adapted their blossom shape to the head morphology of selected pollinating bat species. Despite their various shapes (bellflowers, funnel-shaped blossoms, dish-like flowers, tubular blossoms, labiate flowers, papilionaceous flowers, capitulum flowers, spadiciform flowers, spadiciform brush-like flowers, brush-like flowers, brush-like bellflowers) there is a common feature: the anthers always extend beyond the corolla, so the blossom shape forces the pollinator into a position allowing the pollen to be fixed within the fur (face, neck and shoulders) guaranteeing that any contaminated fur area will most probably touch the stigma of the next blossom to be visited.

Blossom exposition

Blossom exposition represents an important further characteristic of chiropterophilous flowers, facilitating access to the blossoms or inflorescences by shifting them out of the

range of disturbing foliage. Additional aspects are mentioned by v. Helversen (1993): open exposure of flowers give the glossophagine pollinators space for wing movements during hovering flight thereby also minimizing the risk of encountering predators (better visual control and shorter stay). This is achieved in several ways (van der Pijl 1957):

Flagelliflory or Penduliflory

Here, the host plants develop one or more long thin stalks of the inflorescence which is usually pendulous but may sometimes point off the stem almost horizontally. The length of the flagellae varies between 0,6 and 5 m!

Cauliflory

The blossoms are arranged along the stem or along the main branches, also facilitating approaches of the bats (van der Pijl 1936). Example: *Ceiba pentandra*.

Pincushion blossoms

In this configuration, the inflorescences are arranged spherically emerging everywhere from the foliage.

Towering individual inflorescences

As the herbaceous plant does not grow very tall (e.g. *Agave*), it develops a (tree-shaped!) inflorescence and increases probability of becoming exclusively pollinated by bats.

Developing storeys

By arranging the leaves in distinct storeys, the inflorescences are separated from the remaining vegetation area (*Ceiba*).

Diet of various New World nectar feeding bat genera

Analysis of stomach contents in captured specimens revealed some information on their diet. Additionally, many captured bats still carry pollen in their fur (especially around the muzzle, but also on the shoulder or on the neck) allowing to identify or at least to draw conclusions about the plant species they visit.

Lionycteris: Although the diet of *L. spurrelli* is still unknown, it may resemble that of *Lonchophylla* (Gardner 1977). In Peru, one specimen of *L. spurrelli* was captured among blooming Cashew trees (Tuttle 1970).

Lonchophylla: According to Walker et al. (1964), *Lonchophylla* feeds on blossoms, taking in nectar, pollen, but also insects and fruit. Similar reports on Panamanian species of *Lonchophylla* were given by Duke (1967) who reported of a diet consisting of nectar, over-ripe fruit, pollen and insects. This may also apply to the remaining species of the genus (Gardner 1977).

In *L. thomasi*, the faeces and the contents of stomach and intestines were analyzed: in five specimens from east Peru Koepcke (1987) found larger amounts of pollen (2 specimens), pulp and seeds of *Piper* sp. (1 specimen), remnants of unidentified fruit (3 specimens) as well as various thoroughly chewed and indeterminable insects (4 specimens). One of the bats contained a yellowish fluid, probably nectar or fruit juice. Another specimen was covered with pollen on its head, breast and on the wing membranes; its faeces also revealed nothing than pollen. Gardner (1977) observed *L. thomasi* at banana blossoms (also in east Peru), and these bats were covered with pollen on their head and shoulders, too.

For *L. mordax* Gardner (1977) reported insects, fruit, nectar and pollen, without, however, specifying the plant diet. For six *L. m. concava* caught in Costa Rica, Howell & Burch (1974) identified the following particles: nectar and pollen of *Mucuna* sp.(1 ind.), nectar and pollen of *Musa* sp.(2 ind.), remnants of lepidopterans (3 ind.).

L. robusta: Pollen, nectar, fruit and insects (Gardner 1977). Wille (1954) considered *L. robusta* as a nectar feeding bat, though stomach analysis of 17 specimens from Costa Rica and Panama by Fleming et al. (1972) revealed 90% insect remnants (unfortunately, only one analysis was usable at all). Howell & Burch (1974) failed to detect any plant material in three specimens of *L. robusta* from Costa Rica, instead they found remnants of Lepidoptera, Coleoptera and Streblidae (= ectoparasites on bats).

Platalina: The diet of *P. genovensium* is unknown; it probably consists of pollen, nectar and insects (Gardner 1977).

Brachyphylla: *B. nana* consumes fruit, pollen, nectar and insects (Gardner 1977; Swanepoel & Genoways 1983). Stomach contents of 43 specimens from Cuba consisted of partly digested pollen grains. One stomach contained butterfly scales, another one fragments of a fly (Silva Taboada & Pine 1969). Furthermore, these authors regularly found individuals whose head, breast and shoulders were powdered with pollen. Consequently, Silva Taboada & Pine (1969) classified *B. nana* as chiefly pollen feeders, probably adding soft fruit and nectar to their diet.

According to Gardner (1977), *B. cavernarum* feeds on fruit and insects, the fruit predominantly being taken from *Manilkara zapota* (Nellis 1971), papaya (*Carica papaya*), mango (*Mangifera indica*), almond (*Terminalia catappa*), royal palm (*Roystonea borinquena*) and *Cordia* sp. (Nellis & Ehle 1977). These authors also reported on captive individuals which took bananas, apples, pears, peaches and melons - but never citrus fruit - apart from the blossoms of *Ceiba pentandra*, *Thespesia populnea*, royal palm and *Hymenaea courbaril*. During field observations, Nellis & Ehle (1977) failed to distinguish between pollen and nectar intake, but most of the faeces beneath their roosts contained pollen (Swanepoel & Genoways 1983).

Erophylla: *E. sezekorni* takes various fruit, pollen, nectar and insects (Gardner 1977). The earliest descriptions on food intake of this species date from the second half of the 19th century (Osborn 1865): fruit of *Cordia alliodora*, whose soft parts are licked up. Hall & Kelson (1959) called this species "Buffy Fruit Bat". Silva Taboada & Pine (1969) analyzed the stomach contents of 30 *E. sezekorni* from Cuba: in all individuals they found partly digested pollen grains. Three of them contained seeds of *Hohenbergia* (Bromeliaceae); in four specimens they detected insect remnants, including parts of an elaterid beetle (*Conoderus*, Elateridae), of a cockroach (Blattidae, Orthoptera) and various undetermined Diptera and Lepidoptera.

Hall & Kelson (1959) called *E. bombifrons* "Brown flower bat"; Tamsitt & Valdivieso (1970), however, reported this species as frugivorous (Gardner 1977).

Phyllonycteris: *P. poeyi* probably feeds on a variety of fruit, pollen, nectar and insects (Gardner 1977). With respect to the tongue anatomy, Allen (1942) supposed *P. poeyi* to eat pulp, fruit juice, pollen and nectar. Silva Taboada & Pine (1969) analyzed the stomach contents of 42 individuals from Cuba and found partly digested pollen masses. Only one stomach contained lepidopteran scales.

Glossophaga: Presumably due to its conspicuously elongate tongue, *G. soricina* formerly was considered a blood feeder. Later it was supposed to eat insects, until Goodwin & Greenhall (1961) revealed that it feeds on nectar, soft fruit and possibly on seeds (Husson 1962). Gardner's (1977) substantial information on the diet of this genus did not only mention nectar, flower parts (blossom constituents) and fruit, but also insects. In captivity (large flight cages) *Glossophaga* hunted and ate insects deliberately; and insects were also the favourite food of captive individuals having been kept for 14 months in El Salvador,

showing, by the way, some interesting shifts in diet preference: prior to the rainy season, the animals preferred honey water, during the rest of the time they liked insects most. Captive *Glossophaga* accepted honey water or fruit juice taking it from a shallow bowl during hovering flight (Novak & Paradiso 1983). Having analyzed the stomach contents of 217 individuals from Costa Rica and Panama, Fleming (1972) described *Glossophaga* as an omnivorous genus. Only 38 stomachs were completely empty, the remaining contained 34% plant material and 66% insect remnants. This also corresponds to the results of Alvarez & Gonzalez (1970) from Mexico where 61% of 174 stomachs examined did not contain any pollen at all. It is, nevertheless, worth mentioning that from all Glossophaginae studied so far, *G. soricina* showed the greatest variety of different pollen grains (deriving from at least 34 plant families).

For *G. commissarisi* from Costa Rica, Howell & Burch (1974) reported remnants of lepidopterans, fruit (*Acnistus*) as well as pollen and nectar of *Musa* and *Mucuna*. Insects, fruit, pollen and nectar are noted by Gardner (1977).

G. longirostris: Insects, fruit, pollen, nectar and probably other blossom parts (Gardner 1977). Wille (1954) and Valdivieso & Tamsitt (1970) considered *G. longirostris* a nectarivorous species. Goodwin & Greenhall (1961) reported a diet of nectar and pulp, fruit juice and, occasionally, insects.

Monophyllus: Up to now no reliable reports. McNab (1971), Phillips (1971) and other authors supposed *Monophyllus* to feed on soft fruit or nectar, possibly on insects, too. Tamsitt & Valdivieso (1970) failed to sustain captive specimens of *M. redmani* by means of banana pulp and sugar water, as the bats refused any food. For *M. plethodon* there is no information available.

Lichonycteris: Up to now hardly reliable reports. According to Tuttle (1970) and Handley (1976), the development of snout, tongue and molars support to assume that the members of this genus feed on nectar, pollen and probably fruit. Tamsitt & Valdivieso (1961) classified *Lichonycteris* as fruit- and nectar feeders. Carter et al. (1966) reported two specimens they captured next to a night-blooming plant in Guatemala carrying pollen on their fur and on the tail membrane.

Leptonycteris feeds on nectar, pollen, fruit and insects (Novak & Paradiso 1983), the latter comprising only a small proportion and thus may have been eaten accidentally along with the nectar and pollen (Hoffmeister 1957). On the other hand, Rasweiler (1977) pointed out the significance of insect consuming for a healthy diet. As Walker (1964) assumed, the long snout reaches the spine-free parts of cactus fruit; the canines are used to rip the pericarp, and the juice is licked up with the tongue. This genus is characterized by accumulations of yellow or red faeces beneath the roosts, pointing to a diet of pollen, nectar and fruit juice. Correspondingly, Dalquest (1953) reported on *L. nivalis* he captured in San Luis Potosi, Mexico, their stomachs filled with viscous, bright red fruit juice .. "almost certainly the juice of the fruit of the organ cactus". Blossoms of *Agave scabra*, *A. chisosensis* and *A. lechugilla* (Easterla 1972), *Agave schottii* and *Carnegie gigantea* (Cockrum & Hayward 1962) are also reported. The stomachs of 13 *L. nivalis* from Michoacán and Hidalgo, Mexico, contained pollen grains of 22 identified plant species from the genera *Agave*, *Ipomoea*, *Cleome* and *Myrtillcactus* (Alvarez & Gonzalez Q. 1970). *L. yerbabuenae* has been observed on the blossoms of *Malvaviscus*, on blossoms and fruit of cactus and presumably also on the blossoms of *Datura stramonium* (jimsonweed) (Novak & Paradiso 1983; Davis 1974; Schober 1984).

On *L. curasoae* confirmed reports are not given yet, but this species probably feeds similar to other species of its genus (Gardner 1977).

Anoura: According to Nagorsen & Tamsitt (1981), this genus is characterized by opportunistic insectivory, additionally feeding on pollen and nectar.

A. caudifer takes fruit, nectar, pollen and insects (Gardner 1977). As Sazima (1976) reported, *A. cultrata* picks insects from the substrate (foliage gleaner, Wilson 1973). The stomachs of four individuals from Venezuela contained both insect fragments and a creamy fluid. Eight specimens from Panama contained yellow, white and greenish masses, respectively and in two cases unidentified insects. 18 individuals from Colombia had pollen and plant fibres in their stomachs (Tamsitt & Nagorsen 1982). Both individuals Starrett (1969) based on his description of *Anoura werckleae* carried Hibiscus (*Wercklea lutea*) pollen in their fur. *A. cultrata* from Costa Rica was described to eat pollen and nectar (Laval & Fitch 1977); whereas Howell & Burch (1974) found lepidopterans in the stomachs.

Gardner (1977) gave a list of various plants whose blossoms were known by several authors to have been visited by *Anoura*: *Vochysia*, *Symbolanthus latifolius*, *Purpurella grossa*. Additionally, he emphasized the high percentage of insect food in *A. geoffroyi*, pointing to the fact that some of these blossoms do not give any nectar at all so that the bats probably visit them just because of the insects which are attracted by the scent (Goodwin 1946). This is supported by Alvarez & Gonzalez Q. (1970) who found pollen in more than the half of 69 specimens from Mexico; most of this pollen came from entomophile plants. So, they considered *A. geoffroyi* an insectivorous species with occasional pollen intake.

Up to now there are no reports on food intake of *Anoura latidens* available.

Hylonycteris: Insects, pollen and nectar (Gardner 1977). Goodwin (1946) supposed *H. underwoodi* to visit flowers; Hall & Kelson (1959) reported on nectar consuming, and fruit remnants of the jobo plum (*Spondias lutea*) they detected beneath a day shelter in Veracruz, Mexico, gave evidence of frugivory (Hall & Dalquest 1963). Carter (1966) found pollen grains on rump and uropatagium of a specimen he caught in Guatemala next to night-blooming flowers. There is a description from Tabasco, Mexico, by Villa-R. (1967) of one specimen with cocoa pollen (*Theobroma cacao*) on its whiskers and head fur. Analysis of stomach contents by Alvarez & Gonzalez Q. (1970) revealed exclusively pollen (*Lonchocarpus* 99,8%, only 0,2% *Agave* and *Pinus*) for two *H. underwoodi* from Chiapas, Mexico. Early reports on insectivory were given by Howell & Burch (1974) who found remnants of lepidopterans in one specimen from Costa Rica.

Scleronycteris: Most probably fruit, pollen, nectar and insects; up to now no information on the feeding ecology (Gardner 1977).

Choeroniscus: Presumably pollen, nectar and insects (Gardner 1977); no valid information available yet. In his description of *C. godmani*, Villa-R. (1967) relied on analysis of stomach contents by Goodwin & Greenhall (1961) for *C. intermedius* from Trinidad Island: "Microscopical examination of the stomach contents of one specimen, however, revealed some minute particles that are possibly honey or fruit juice, many fragments of a coleopterous insect, and numerous brown and white, hair-like strands, probably either from insects or from fruit. This specimen, at least, had fed to a large extent on insects". Having examined four individuals from east Peru, Koepcke (1987) detected nectar in the intestines of two specimens, pollen in one of them and in three cases some Coleoptera and Hymenoptera as well as indeterminate plant material in two *C. intermedius*.

Choeronycteris: Fruit, pollen. Nectar and probably insects (Gardner 1977). Several authors described *C. mexicana* as a flower-feeding bat (Dalquest 1953; Park & Hall 1951; Wille

1954; Hall & Kelson 1959). Its host plants are reportedly *Lemaireocereus*, *Myrtillocactus* and *Ipomea arborea* (Villa-R 1967) as well as *Ceiba* and *Agave* (Alvarez & Gonzalez 1970). All the results on stomach contents and the host plants identified so far (all of them are specialized chiropterophilous night-blooming plants) convinced Alvarez & Gonzalez (1970) of the fact that *C. mexicana* is an obligate nectar feeder. Until now, there has been no evidence on insectivory. Schaldach & McLaughlin (1960) detected *C. harrisoni* at banana blossoms (*Musa* sp., therefore named the genus *Musonycteris*). Gardner (1977) mentioned some pollen at the head and muzzle in some of the individuals having been captured at a small banana plantation in Colima, Mexico, and which had been included in the first description by Schaldach & McLaughlin.

As a conclusion, all taxa mentioned here have been either proved to feed on flowers or they are most probably nectar feeders. As already stated in the introduction, the short-skulled forms (*Glossophaga*, *Lionycteris*) but also *Anoura* frequently take insects, predominantly beetles and moths. On the other hand, there is no evidence yet for insectivory in taxa with an extremely elongate skull (*Choeronycteris*).

Sensory systems / Orientation

Acoustic perception; echolocation

Like all Microchiroptera, the nectarivorous phyllostomatids perform an efficient echolocation. Especially the nose leaf certainly contributes to sound emission. Presumably the lancet (upper part of the nose leaf) is necessary to focus the emitted sound bundles vertically (Hartley & Suthers 1987).

Analyzing the sounds of various phyllostomid species, Griffin & Novick (1955) managed to prove that echo location is also essential in orientation of nectar feeding bats. Further investigation revealed the orientation pulses of the flower bats to be frequency-modulated signals of 1-5 ms length (FM-sounds of the vespertilionid type).

Experimental investigation on the significance of acoustic perception in foraging was performed by Howell (1974): the flower visiting species e.g. *Glossophaga soricina*, *Anoura geoffroyi* and *Choeronycteris mexicana* emit 5-10 short searching pulses per second, each of them lasting 0.5-2 ms. When approaching an obstacle (or aiming at a blossom) the number of emitted orientation pulses increases to 30 signals per second, thus enabling to assess distances precisely even at flight velocities of several meters per second. When the bats were further tested on their ability to avoid obstacles, the predominantly insectivorous species complied with the abilities of other Microchiroptera (*Myotis*), whereas the species mainly interacting with chiropterophileous plants perceived only much stronger wires. Determination of acoustic perception thresholds by means of shunting off the cochlea potential did not reveal any diet specific differences but indicated a polyphyletic origin of the subfamily (Howell 1974).

The importance of echolocation in pollinating bats is also documented by the development of the acoustic cerebral areas (Baron & Jolicoeur 1980). Their progression indices come quite close to those of insectivorous Microchiroptera.

Optical sense

Though in all microchiropterans a highly developed echolocation apparatus proves dominance of the acoustic system over the remaining senses, in certain situations it may be replaced or complemented by optical perception. So, visual orientation becomes

important beyond range of sound, for instance in order to identify large, far objects, land marks or the horizon (Suthers 1966; 1970).

All phyllostomids have well developed eyes with efficient differentiation of brightness and shapes. Flower bats always keep their eyes open, when active. Some nectar feeding species (e.g., *Anoura caudifer*) are reported to have a tapetum (v. Helversen 1993) and perform a well developed ability for pattern recognition. It is, by the way, interesting for this respect that some bat flowers developed conspicuous patches for "close range guiding" the bats in approach (Dobat & Peikert 1985). But the absence of retinal cones gives no evidence for colours to be discriminated (Suthers 1970). Anatomically however, the optical areas in brain cortex are clearly less developed than the acoustic centers.

Olfactory sense / Olfactory perception

In fruit feeding bats, the leading role of food detection by olfactory sense has been satisfactorily documented (for both Megachiroptera and frugivorous phyllostomids). This is also confirmed in brain anatomy by relative size of the Bulbus olfactorius. Although this structure turns out smaller in nectar feeding New World Microchiroptera, it still remains considerably larger than in species which exclusively feed on insects having the smallest Bulbi olfactorii among all Chiroptera (Dobat & Peikert 1985). Chiropterophile blossoms are often characterized by a slightly sour, musty scent which is apparently responsible for attracting pollinators. According to observations by Vogel (1958) a sudden breeze finished pollinating activity immediately, which also gives evidence of the well developed olfactory abilities of the nectar feeders. Olfaction does not only serve for long-distance orientation but is also important in short-distance target discrimination - detection of the nectarbearing flowers (v. Helversen 1993).

Reproductive Biology

Reproductive data of nectar feeding bat species is mainly based on comments on the sexual status of captured specimens. Pregnant females give information about size and weight of fetus; lactation periods are easily recorded from the dates of netted females carrying juveniles. Development of youngsters, but also relative weight and measures of gonades (enlargement of uterus, ovarian follicles, appearance of corpora lutea in females; size of testicles in males) allow conclusions on seasonal breeding patterns by comparing the different information to the date of capture.

So far, we still have poor knowledge on the reproductive behavior of nectarivorous phyllostomid chiropteres: among the species of the tropical rain forest, breeding all over the year without marked seasonal periods is common, whereas those inhabiting subtropic (more arid) zones or andine mountain forests show one definitely seasonal or two separate (bimodal) reproductive periods per year.

Lionycteris: Tuttle (1970) reported a pregnant female of *L. spurrelli* containing one single embryo captured in Peru on August 5th.

Lonchophylla: Wilson (1979) took pregnant *L. mordax* in Costa Rica as well in March as in August. Also in Costa Rica LaVal & Fitch (1977) found pregnant *L. robusta* in February, May, August and October; one lactating female in January. According to Koepecke (1987) the reproductive period of *L. thomasi* in amazonian Peru occurs during the dry season. She netted sexual inactive bats in June, October, November and December.

In contrast a female collected in July was pregnant. In September, a family, watched in field by the same author, nursed a nearly full grown juvenile which still stayed with its parents during following January. At Manaus, Reis (1981) found sexual active males during dry season and at the beginning of the rainy season.

Platalina: No data on reproductive biology yet available for this very rare endemic peruvian genus.

Brachyphylla: Twelve female *B. nana* trapped on Middle Caicos Island in March all were pregnant, with crown rump length of fetuses between 24 and 34 mm (Buden, 1977). In contrast females collected on Hispaniola in December and late August were not pregnant, but one of the August females was lactating. The testes of one male netted during the same time were only 3 mm long (Klingener et al. 1978). On Cuba, female *B. nana* carried embryos from December through May, lactation occurred from May to August; the diameter of the testes of males varied from 5 to 9 mm in specimens caught in December (Silva-Taboada 1979).

On Puerto Rico, nursing females of *B. cavernarum* have been collected on 5th July, but there was no information about the young (Anthony 1918). Later studies on 25 females (small uteri, no suspicious ovarian follicles) and males (testes 4-6 mm) from St. Croix gave no evidence for reproductive activities in December (Bond & Seaman 1958). Walker et al. (1964) mentioned nursing females from Puerto Rico in July; later reports of the same authors (1975) stated pregnant females in February and a lactating female in April. On St. Croix, pregnant females were observed in March, and it was here that Nellis (1971) collected a nursing female in April. Detailed observations by Nellis & Ehle (1977) on a colony on St. Croix in the time between May and June showed the colony consisting of pregnant females only, which give birth to their young during that time.

Baker et al. (1978) collected 15 adult females on Guadeloupe in July; none of them was pregnant but three were obviously nursing. Males netted at the same time showed testes of 4-6 mm length. Thus *B. cavernarum* probably has a more synchronized reproductive cycle than, for instance, *Artibeus*. Also Wilson (1979) suggested a synchronized, probably bimodal reproductive cycle for *B. cavernarum*, a second period of parturition occurring annually at least in some populations.

Erophylla: Eleven (of approximately twenty) female *E. sezekorni* taken in Cuba on 26th and 28th February contained small embryos (Anthony 1919). Buden (1976) summarized the reproductive behavior of this species: "Most prenatal development takes place during the first part of the year and parturition probably occurs in early summer." Females bearing young embryos were collected in early and late February. Individuals with well developed fetuses were obtained in April and May. Lactating females were collected in June and many immatures in July. Nearly adult youngsters were found in August. Thus *E. sezekorni* seems to be a seasonal breeder possibly bearing only one single offspring per year.

Pregnant *E. bombifrons* were captured on Puerto Rico by Valdivieso & Tamsitt (1971) in June and July.

Phyllonycteris: Parturition in *P. poeyi* takes place mainly in June (Novak & Paradiso 1983). Goodwin (1970) trapped a pregnant female in January; Baker et al. (1978) reported three gravid specimens from Haiti on 17th December.

Glossophaga: Nursing colonies containing several hundreds of female *G. soricina* and their young were found in San Luis Potosi (México) during midsummer; in Guerrero (also

Mexico) in midsummer the studied colonies were formed of both sexes. My own observations in Ecuador during July 1983 dealt with both sexes within the same large colony including pregnant and lactating females. In Veracruz (Mexico) Hall & Dalquest (1963) found mixed colonies with more than 1000 individuals.

According to Wilson (1974) who compiled data of pregnant females for all months over the year *Glossophaga* occurred to be polyestric at most of the collecting sites.

Reproductive patterns and ontogeny of *G. soricina* have been studied extensively (Bleier 1979; Rasweiler 1972, 1974, 1979; Wilson 1979) and are reported by Alvarez, Willig, Knox Jones & Webster (1991): ovulation is spontaneous and usually one ovum is released per cycle. Ovulation may occur from either ovary, but tends to alternate between both. Menstruation and ovulation take place at approximately the same time. The two-cell development stage is achieved on day 2 or 3 after fertilization, the 8-cell stage by days 5 to 7, the 32-cell stage by day 8, and the blastocyst stage by day 10. The embryo is contained within the ampulla of the oviduct until day 12 or 13, by which time the Zona pelliculosa usually is lost. Implantation occurs in the uterotubal junction on days 12 to 14. Rasweiler (1974) divided the process of implantation into eight stages and Hamlett (1935) described the embryonic growth thereafter. *Glossophaga* shows a discoidal and haemochorial placenta. The occurrence of menstruation and interstitial implantation suggests that *Glossophaga* might possess considerable potential for development as an animal model in human reproductive research (Rasweiler 1974).

Wilson (1979) found pregnant *G. commissarisi* in January, February, April, July and September. This indicates a bimodal polyestrus. LaVal & Fitch (1977) report a seasonal polyestrus on *G. commissarisi* in Costa Rica, their data on pregnant females refer to February/March and October.

According to Wilson (1979) *G. longirostris* nurses its youngsters during rain period; the data of capture show pregnant or lactating females from February to September.

Webster (1983) collected pregnant *G. leachii* (containing one single fetus each) in February, April, June, July, August, September and November. Nursing mothers were obtained in February, March, June and November.

G. mexicana is supposed to be monestric, the duration of breeding season remains unclear: a pregnant female was collected in March, a lactating specimen in May. Other females caught in February, March, April, May and August gave no evidence of reproductive activity. Four males taken in June had testicle diameters of 4 mm; the testes of another male captured in July measured 8x6 mm (Webster & Jones 1985).

Monophyllus: Buden (1975) reports pregnant *M. redmani* (each with a single fetus): on 28th January he obtained one female on Middle Caicos (Bahamas), its fetus with crown rump length of 20 mm. On 3rd December and 24th February (on Hispaniola) three specimens containing fetuses of 16-19 mm length. One from Puerto Rico was gravid on 5th February.

Pregnant females of *M. plethodon* were taken on Dominica between 24th March and 22nd April. Crown-rump-length of fetuses varied from 17 to 24 mm; the larger ones were caught later. Males captured at the same time had testes 4-4.5 mm long (Homan & Jones 1975).

Lichonycteris: On Costa Rica, Gardner, LaVal & Wilson (1970) reported a nursing female collected together with a male young on 9th January. Another specimen taken in March contained a 14 mm embryo. In Guatemala pregnant females are also dated in February (Wilson 1979).

Leptonycteris: These bats form large colonies homing more than 1000 individuals. In their northern habitats nursing females aggregate during springtime into breeding colonies numbering thousands of animals; Smith & Genoways (1974) reported a colony of *L. curasoae* on Isla Margarita (Venezuela), containing almost 4000 females and nearly adult juveniles. In November no more juveniles but pregnant females and reproductive males were found.

In Texas and Mexico, young *L. nivalis* appear to be born during summer (Davis 1974). In contrast Wilson (1979) caught pregnant *L. sanborni* in Mexico as well in February, March, April as in July, September und November.

Anoura: Pregnant and lactating *A. caudifer* were collected in January, February, May, June and November by Carter & Jones (1978). Gardner (1970) reported on *A. cultrata* in Columbia: a female taken in August carried a fetus of 28.5 mm length. Two specimens captured in west central Colombia on 17th July aborted well developed fetuses (20 and 21 mm long); and lactating females were found on 30th and 31st July (Lemke & Tamsitt 1979). In southwestern Colombia the same authors collected three females on 10 August, each contained a single embryo (11-14 mm crown-rump length). In Peru Carter (1968) took lactating females on 16th und 21st August. Usually female *A. cultrata* bear a single offspring, but there is also a report on twins (Tamsitt & Nagorsen 1982). The data obtained of captive males in Costa Rica revealed sexually active individuals (testes > 6 mm) in February, May and July; in Panama in February; and in Columbia in May, July and early August. Testes of males collected in March and April in Venezuela and in late August in Columbia and Peru were smaller (1-4 mm) than those of specimens taken in other months (Tamsitt & Nagorsen 1982).

The data for *A. geoffroyi* compiled by Wilson (1979) suggest this species on Trinidad to form colonies of separated sexes within the same caves during particular seasons. In June there were 20 males and 25 females in one cave; in October 29 males and only one female; in November 32 male and 56 female bats. In this region *A. geoffroyi* obviously give birth to its offspring at the end of raining season, so pregnant females were found in November. In Nicaragua pregnant females were taken in July, in Costa Rica in March and in Peru in June and July. In Mexico nursing mothers were found im July, November and December (Carter & Jones 1978; Wilson 1979).

Hylonycteris: Carter (1966) mentioned a lactating female from Guatemala, captured on 2nd March. For Jalisco (Mexico) there are data by Phillips & Jones (1971) on three pregnant female *H. underwoodi* collected in early September each bearing a single fetus of 14, 18 und 21 mm crown-rump length. In December Hall & Dalquest (1963) took a male with "small testes"; Gardner (1970) describes the testes of three males caught in Costa Rica in February and one April and July as "moderately enlarged, averaging in 2.7x2.3 mm".

Choeroniscus: Pregnant females of *C. godmani* were netted in Mexico during May, in Sinaloa (Mexico) in July, in Nicaragua during March and in Costa Rica in December, January, February and March (LaVal & Fitch 1977; Wilson 1979).

During her field work Koepcke (1987) watched a female *C. intermedius* with a newborn baby in the amazonian rainforest in Peru in late June. Animals captured in the months of August, November und December showed no reproductive activity. On Trinidad a pregnant female is noted in August, probably this species is bimodal polyestric (Tuttle 1970).

Table 3: Chromosomal data on New World nectar-feeding bats (adapted from Baker 1979)

Notes

Genera and species are given in alphabetical order (inclusive species without informations)

Key to abbreviations: 2n = diploid chromosome set; FN = number of chromatids; M = metacentric; SM = submetacentric; ST = subtelocentric; A = acrocentric.

| Taxon | 2n | FN | X | Y | Y ₂ | Autor | no |
|--------------------------------|----|----|----|----|----------------|----------------------------|----|
| <i>Anoura brevirostrum</i> | - | - | - | - | - | - | - |
| <i>A. caudifer</i> | 30 | - | - | - | - | Yonenaga 1968 | - |
| | 30 | 56 | SM | A | - | Baker 1973 | - |
| <i>A. cultrata</i> | 30 | 56 | SM | A | - | Baker 1979 | 1 |
| <i>A. geoffroyi</i> | 30 | 56 | SM | A | - | Baker 1967; Hsu et al.1968 | - |
| | 30 | - | SM | A | - | Baker & Hsu 1970 | 3 |
| | - | - | SM | - | - | Pathak & Stock 1974 | - |
| <i>A. werckleae</i> | - | - | - | - | - | - | - |
| <i>Choeroniscus godmani</i> | 19 | 32 | SM | ST | A | Baker 1967 | 5 |
| | 19 | - | - | - | - | Hsu et al. 1968 | 5 |
| | 19 | 32 | SM | A | A | Baker 1970a | 1 |
| | 20 | 36 | SM | - | - | Patton & Gardner 1971 | 1 |
| | 20 | 36 | - | - | - | Baker 1979 | - |
| <i>Ch. inca</i> | - | - | - | - | - | - | - |
| <i>Ch. intermedius</i> | 20 | 36 | - | - | - | Baker 1970a | - |
| | 20 | - | - | - | - | Baker 1973 | - |
| | - | - | SM | - | - | Pathak & Stock 1974 | 1 |
| | 20 | 36 | SM | A | - | Stock 1975 | 1 |
| <i>Ch. minor</i> | - | - | - | - | - | - | - |
| <i>Ch. periosus</i> | - | - | - | - | - | - | - |
| <i>Ch. mexicana</i> | 16 | 24 | - | - | - | Baker 1967; Hsu et al.1968 | 1 |
| | 16 | 24 | SM | SM | - | Baker 1973 | - |
| <i>Glossophaga alticola</i> | 32 | 60 | M | A | - | Baker 1967 | 4 |
| <i>G. commissarisi</i> | 32 | 60 | M | A | - | Baker 1967; Hsu et al.1968 | 5 |
| <i>G. longirostris</i> | 32 | 60 | M | A | - | Baker 1979 | - |
| <i>G. soricina</i> | 32 | 60 | M | A | - | Baker 1967; Hsu et al.1968 | 14 |
| | 32 | 60 | M | A | - | Baker & Hsu 1970 | 4 |
| | 32 | 60 | SM | A | - | Baker 1970a | 1 |
| <i>Hylonycteris underwoodi</i> | 16 | 24 | - | - | - | Baker 1973 | - |
| <i>Leptonycteris curasoae</i> | - | - | - | - | - | - | - |
| <i>L. sanborni</i> | 32 | 60 | M | A | - | Baker 1967; Hsu et al.1968 | 5 |
| <i>L. nivalis</i> | 32 | 60 | - | - | - | Baker 1973 | - |
| <i>Lichonycteris degener</i> | - | - | - | - | - | - | - |
| <i>L. obscura</i> | 28 | 50 | SM | A | - | Baker 1973 | 1 |
| | 24 | 44 | - | - | - | Baker 1979 | 2 |
| <i>Lionycteris spurelli</i> | 28 | 50 | SM | A | - | Baker 1979 | 1 |
| <i>Lonchophylla concava</i> | - | - | - | - | - | - | - |
| <i>L. hesperia</i> | - | - | - | - | - | - | - |
| <i>L. mordax</i> | - | - | - | - | - | - | - |
| <i>L. robusta</i> | 28 | 50 | SM | A | - | Baker 1973 | - |
| <i>L. thomasi</i> | 30 | 34 | - | - | - | Baker 1973 | - |
| | 32 | 38 | - | - | - | Gardner 1977 | - |
| <i>Monophyllus plethodon</i> | 32 | 60 | SM | A | - | Baker 1979 | 3 |
| <i>M. redmani</i> | 32 | 60 | SM | A | - | Baker & Lopez 1970b | 7 |
| <i>Musonycteris harrisoni</i> | - | - | - | - | - | - | - |
| <i>Platalina genovensium</i> | - | - | - | - | - | - | - |
| <i>Scleronycteris ega</i> | - | - | - | - | - | - | - |

Choeronycteris: There is an outline by Wilson (1979) on *C. mexicana*: in Mexico females are pregnant in spring. Those which migrate to Arizona and New Mexico there give birth to their young during June/July. This species is monestric, but may have a second breeding season per year, for in Jalisco a pregnant female has been caught in September (Watkins & al., 1972). According to Barbour & Davis (1969) parturition in *C. mexicana* takes place within 15 min. Newborn young are well developed and also furred.

Cytology

The New World Phyllostomatidae have been subject to thorough cytological examination. Above all, the team of R.J. Baker, Texas Tech University in Lubbock, Texas, published numerous karyological and cytogenetic papers on this subject. There are also detailed chromosomal data on nectarivorous genera (cf. tab.3, from Baker 1979).

It is striking that even species within the same genus often show considerable differences in their karyotype, Warner (1983) referred to this phenomenon as "Karyotypic megaevolution". It is, therefore, hardly surprising that by means of cytogenetic analysis completely contradictory relationships were postulated by different authors, one example being parallel evolution of a multiple sex chromosome system (Patton & Gardner 1971) in *Carollia* and *Choeronycteris*: as the males in both genera have a XYY-configuration, they were supposed to be related (Hsu et al. 1968). Further studies emphasized the weak points of the "G-Banding Patterns", thus preferring the C-banding analysis (heterochromatin technique). Here, anyway, specimens from both genera showed the original XY type, so chromosomal configuration seems to undergo comprehensive evolutionary changes.

MATERIAL AND METHODS

Material

This study is based on skulls and specimens preserved in alcohol. The material comprises 29 genera from the subfamilies Phyllostominae, Carollinae, Lonchophyllinae, Brachyphyllinae, Phyllostomyinae and Glossophaginae.

Some of the individuals examined were captured during a three-week study visit to Ecuador (July 1983), visiting locations in the surroundings of Quito (San Antonio de Pichincha, 2100 m above mean sea level), in the secondary forest of West Ecuador (Chontilla) and in the rain forest area east of the Andes (Rio Cuyabeno, Amazon headwater region, Cueva de Jumandi). In the course of this journey, the available bat collection of the Museum of the Escuela Politecnica Nacional (MEPN), Quito, could be accessed and studied.

Some of the genera worked on here are known only by very few specimens. Thus it was necessary to examine some of the extremely rare material personally in the collections. Consequently, the following museums were visited:

- Zoologische Staatssammlung München
- Naturhistorisches Museum Wien
- Rijksmuseum voor Natuurlijke Historie, Leiden
- Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn

- Naturhistorisches Museum Basel
- British Museum of Natural History, London
- American Museum of Natural History, New York.

Additional material was kindly lent by the following museums and collections:

- American Museum of Natural History, New York, (AMNH)
- British Museum (Natural History), London, (BMNH)
- Collection Dr. Juliane Diller, geb.Koepcke, München, (JK)
- Musée d'Histoire Naturelle, Genève, (MHNG)
- Naturhistorisches Museum, Basel, (NHMB)
- Naturhistorisches Museum der Alexander v. Humboldt Universität zu Berlin (MNHUB)
- Naturhistorisches Museum, Wien, (NHMW)
- Museum Kopenhagen
- Rijksmuseum voor Natuurlijke Historie, Leiden, (RMNH)
- Royal Ontario Museum, Toronto, (ROM)
- Senckenberg Forschungsinstitut und Naturhistorisches Museum, Frankfurt, (SMF)
- Smithsonian Institution, United States National Museum, Washington, D.C. (USNM)
- Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, (ZFMK)
- Zoologisches Institut und Zoologisches Museum der Universität Hamburg, (ZIM)

A complete list of all material is given in the appendix.

Methods

Descriptions

Gross morphology

Both alcohol preserved specimens or skins, were examined using a stereomicroscope. All descriptions comprised also body size, characteristics of head morphology (nose leaf, auricles, tragus, lower lip) and features of the pelage (colouring, areas of the body, hair shaft) as well as the bones of the wings (metacarpalia, phalanges) and tail length. The insertions of the plagiopatagium at the hind extremities and the shape of the uropatagium are of special diagnostic value.

Skull morphology

Skulls were examined with a stereomicroscope using various magnifications (5x; 12.5x; 30x). For most overviews, five times magnification was sufficient, whereas features of the dentition often required some higher magnification. If possible, the description considered rostrum length compared to total skull length, the skull contours in lateral view as well as the arrangement of the skull basis towards the level of the palate. Development of the zygomatic arches was equally mentioned as were the features of the skull base: pterygoid processes, convexity of pre- and basisphenoid („basisphenoid pits") and basioccipitale.

In all genera, the dentition was documented by dental formulas. The upper incisivi, canini, premolars, molars, lower incisivi, lower canini, lower premolars and lower molars were briefly described referring to specific peculiarities (contour of edges, height of crowns, interdental distances, development of the masticatory surfaces, relative dimensions).

More detailed descriptions of the glossophagine dentition are given by Phillips (1971).

Drawings

All specimens borrowed could be documented by drawings of the skull in dorsal, lateral and basal view. Using a stereo microscope with a drawing projector, the mandibles were drawn in top view and in lateral view. The scale is always 10 mm.

The material examined during museum stays was photographed by means of a macro lens (135 mm) on fine-grain black and white negative film; the drawings were done after these pictures.

Measurements

The preserved skulls were measured by means of a slide caliper (0.02 mm). Any skull measure was taken three times and the mean value was recorded on prepared record forms. The measures are given in fig.2. A table with all values measured can be ordered from the author.

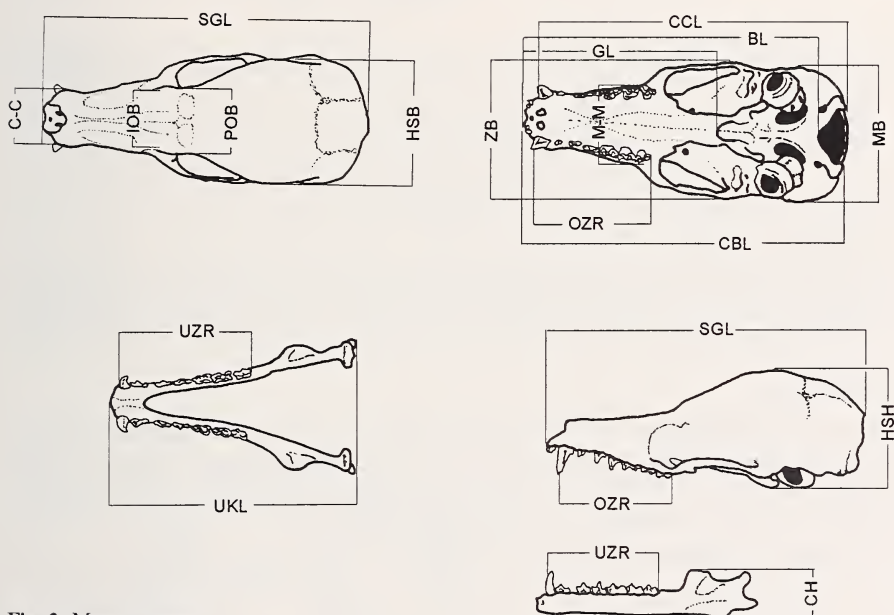


Fig. 2: Measurements

BL = basal length
CBL = condylobasal length
C-C = width over incisivi
CCL = condylocanine length
CH = height of coronoid process
GL = length of palate
HSB = width of braincase
HSH = height of braincase
IOB = interorbital width

MB = mastoid width
M-M = width over molars
OZR = upper tooth row (C-M³)
POB = postorbital width
SGL = total skull length
UZR = lower tooth row (C-M₃)
UKL = mandible length
ZB = zygomatic width; (distance between prs. zygomata)

To see how differences in cranial measures (i.e. "y") depend on skull size (i.e. "x"), I decided to calculate an artificial volume quantity called SIZE. In order to exclude influence of rostral length on the chosen reference quantity, SIZE (=x) is determined by neurocranial measures only (cf. fig.3).

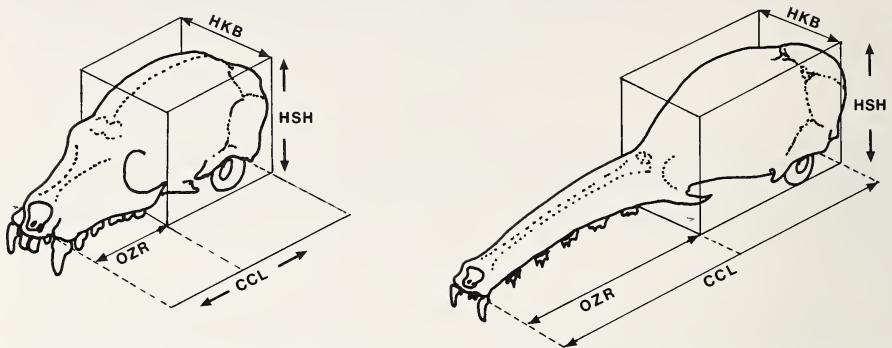


Fig.3: SIZE = (Condylocanine Length minus Upper Tooth Row) * Height of Braincase * Width of Braincase

Calculations

Univariate Analysis

For each skull measures in each species, the mean value and standard deviation was calculated. If possible, males and females were compared to each other as separate random samples (F-test, t-test).

Allometrics

In individuals of different size, allometric calculations allow to distinguish proportional shifts exclusively based on size increase from differences in proportion caused by other reasons. Often, such differences in proportion reveal deviating construction principles which can also be evaluated in a taxonomical respect.

Mathematically, allometrics are recorded by means of the allometric formula:

$$y = b * x^a$$

$$\log y = \log b + a * \log x$$

This causes comparison of measures representing different dimensions: units of length against volume measures. Thus, for allometric analysis instead of the usual regression lines the reduced elliptic major axis of distribution (Rempe 1962) was referred to.

All necessary calculations were performed on a IBM compatible personal computer by means of a regression calculating software written in BASIC (D. Vinyard, after Müller/Kick 1983, see appendix 9.4) as well as DIVA (Ver.2.0), a statistics software by D. Plogmann. All calculations were based on the works of Rempe (1962).

RESULTS

Morphology of the species examined

External morphology

Many of the bats described here resemble each other to an enormous extent and may only be identified by delicate characters. External characters relevant for identification are the development of the uropatagium, the insertion of the wing membrane at the foot or at the tibia, presence and development of a calcar, the length relations of the bones supporting the wings, shape and relative size of the nose leaf or the auricle and the tragus, respectively.

Generally, in all phyllostomid flower bats, the lower lip shows a distinctly V-shaped median notch laterally lined by small warts. The elongate tongue covered with brush-like hairy papillae is clearly visible also in living oder undissected specimens. In all long-faced species an elongate rostrum will attract attention.

Lionycteris

L. spurrelli: Very small bat; forearm length <35 mm. Muzzle imperceptibly elongated compared to non-nectar-feeding phyllostomids. Relatively large nose leaf (wide and short). Auricles small and rounded, dark. Lower lip showing a very small median V-shaped notch of warty bulges with a tip ending ventrally in an unpaired wart (fig.4).

Tragus short with small serrated basal wings (ref. fig.4). Pelage reddish brown to black brown, lighter ventrally (greyish brown); wing membranes darker than fur.

Forearm sparsely haired, very short thumb. Metacarpalia III>IV>V, 1. phalanx III>IV=V. Plagiopatagium inserts distally at the tibia. Uropatagium present. Short tail projecting beyond the wing membrane in its last third and ending with a perceptible stump (fig.4).



Fig.4: *Lionycteris spurrelli*, head, tragus, and interfemoral membrane

Lonchophylla

Resembling in appearance *Lionycteris*, but with distinctly stretched head. Compared to *Lionycteris*, the nose leaf is long and narrow. Auricle rounded, tragus with smooth contours (fig.5).



Fig. 5: *Lonchophylla robusta*, head



Fig. 6: *Lonchophylla* spec., interfemoral membrane

Extensive uropatagium present, short tail, dorsally projecting beyond the wing membrane. Calcar does not reach foot length, plagiopatagium inserts at the ankle joint (fig.6).

L. thomasi: Smallest species within the genus, forearm length 31-32 mm.

L. mordax: Forearm length 34-35 mm.

L. robusta: Forearm length 41-46 mm.

L. handleyi: Largest known species within genus, forearm length 44-48 mm.

Platalina

P. genovensium: Relatively large flower bat, forearm length 48-49 mm. Externally visible elongated head, the smooth nose leaf lacking a median "suture"; two distinct narrow grooves parallel with both basal edges. Forearm and distal part of upper arm naked.



Fig.7: *Platalina genovensium*, interfemoral membrane



Fig.8: *Brachyphylla cavernarum*, head

Well developed uropatagium, the median extension reaching the lower third of tibia. Calcar as long as foot including claws. Plagiopatagium inserts at tarsus. Tail (ca. 8 mm) present, projects dorsally in first quarter of the uropatagium as a touchable stump (fig.7).

Brachyphylla

Comparatively very large bats, head not visibly elongated. Nose leaf without spear but showing two concentrically lining, deep circular wrinkles around the nostrils. Thus, the face (fig.8) resembles that of the Desmodontinae (true vampires). Strikingly strong thumbs and large, strong feet. The uropatagium forms a well developed interfemoral membrane. No externally visible tail, no calcar, the plagiopatagium inserts at the tarsus. Pelage colour varies, with head and back usually light brown, yellowish to ivory, ventral side most often brown (lighter than dorsally). The (naked) plagiopatagium is darker, almost black.

B. nana: Forearm length 56-59 mm.

B. cavernarum: Forearm length 63-69 mm.

Erophylla

Large blossom bat with conical, moderately elongate muzzle. Nose leaf without spear, similar to *Brachyphylla*, but more delicate and with small central tip. Resembles the nose of Old World Rhinopomatidae ("pig snout"). Uropatagium restricted to a narrow fringe being distinctly projected by the tail. Very short calcar.

E. sezekorni (fig.9): Forearm length 45-49 mm. Long thumb (1. phalanx I = 7mm). Metacarpalia: III>IV<V (III >=V); 1. phalanges: III > IV >=V. Uropatagium short, marginal outline wedge-shaped, running from very short calcars to the tail tip. Plagiopatagium inserts at distal tibia immediately above the ankle joint. Pelage coloration pale yellow brown to reddish grey, slightly blotchy ("frosty", "mangy"), ventral view and face lighter. Short tragus with smooth margin.



Fig. 9: *Erophylla sezekorni*, head, tragus, and interfemoral membrane

E. bombifrons (fig.10): Forearm length 46-50 mm, thumb very long (1. phalanx I = 8.5mm); metacarpalia: III>IV>V; 1. phalanges: III>IV; tragus only terminally pointed and with a blunt margin. Short uropatagium, marginal outline semicircular between very short calcars (3.4mm). Tail projects half over this margin. Plagiopatagium inserts at distal tibia immediately above ankle joint. Pelage dorsally reddish light brown to dark brown; slightly lighter ventrally, beige grey; hairs dark only at distal third of the shaft, basal portion light for two thirds.

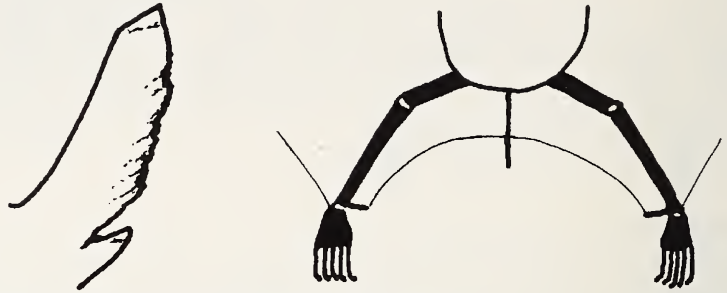


Fig. 10: *Erophylla bombifrons*, tragus and interfemoral membrane

Phyllonycteris

P. poeyi (fig.11): Rather large flower bat, similar to *Erophylla*; forearm length 46-49 mm; with reduced nose leaf lacking a spear; but contours more similar to *Brachyphylla*. Very short uropatagium; tail projects far beyond the margin of uropatagium; no calcar. Plagiopatagium inserts at distal tibia distinctly above the ankle joint. Pelage coloured with a shimmering light grey/beige.

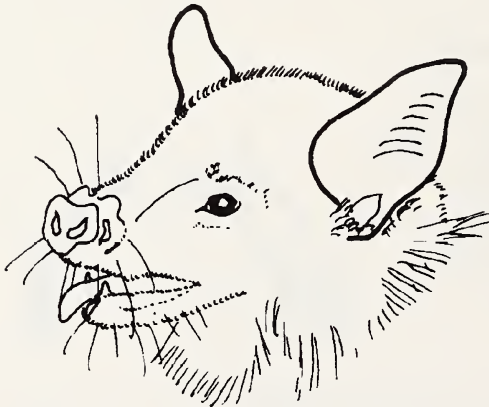


Fig.11: *Phyllonycteris poeyi*, head



Fig.12: *Glossophaga soricina*, head and interfemoral membrane

Glossophaga

Small to medium sized nectarfeeding bats, forearm length 32-42 mm; head with moderately elongate muzzle, small nose leaf. Well developed uropatagium with semicircular fringe; short calcar (<foot length). Short tail, embedded only in first half of uropatagium. Plagiopatagium inserts at ankle joint.

G. soricina (fig.12): Forearm length 34-37 mm.

G. commissarisi: Forearm length 31-35 mm.

G. longirostris: With a forearm length of 36-42 mm largest species of the genus; with rather elongate face (name!). Ears short and rounded; small tragus with smooth contours (fig.13).

G. leachii: Forearm length 35-38 mm (largest Central American species)

G. mexicana: Forearm length 32-36.5 mm.



Fig.13: *Glossophaga longirostris*, tragus

Monophyllus

M. redmani: Medium sized glossophagine bat, elongate muzzle hardly recognizable. Forearm length 34.8-43 mm. Long thumb. Forearm haired in proximal third. Pelage dark reddish brown, "frosty grey" coloured ventrally. Ears short and comparatively pointed; tragus short, with strongly undulated edge and also undulating, notched basal lobe (fig.14).



Fig. 14: *Monophyllus redmani*, tragus

Uropatagium narrow, inner edge running at an acute angle; tail relatively long, distinctly projecting beyond the naked fringe of the tail membrane (fig.15a).

M. plethodon: Usually larger than *M. redmani*. Forearm length 38.8-45.7 mm. Uropatagial fringe semicircular (fig.15b).

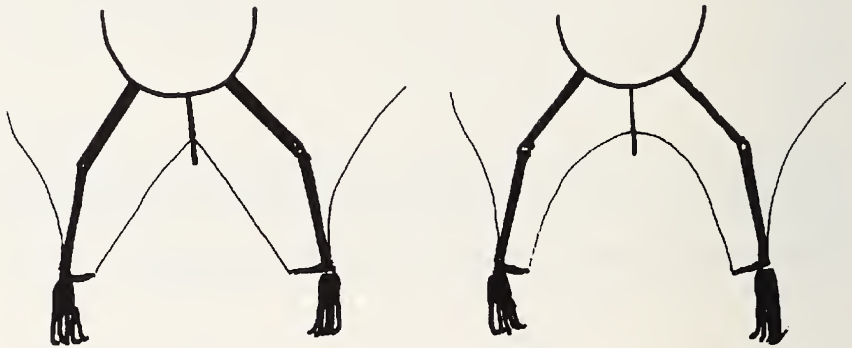


Fig.15: Interfemoral membranes of *Monophyllus*: a: *M. redmani*, b: *M. plethodon*

Leptonycteris

Comparatively large flower bats with moderately elongate muzzle appearing blunt in living specimens compared to other glossophagines. Nose leaf with short triangular spear, tragus with smooth contours. Forearm naked; pelage coloration usually light brown. Uropatagium reduced to a 3-4 mm thin fringe running at an acute angle. No externally visible tail (but nevertheless present with three vertebrae).

L. nivalis: Forearm length 55.4-59.5 mm. Metacarpale III shorter than phalanges III; uropatagial fringe covered with conspicuous hairs, 3-4 mm long.

L. yerbabuenae (fig.16): Forearm length 50-54.8 mm. Metacarpale III as long as phalanges III; uropatagial fringe almost naked.

L. curasoae: Same size as *L. yerbabuenae*, uropatagial fringe sparsely haired.



Fig.16: *Leptonycteris yerbabuenae*, head, tragus, and interfemoral membrane

Lichonycteris

L. obscura (fig.17): Very small nectar feeding bat, forearm length 32.4 mm; with short pointed muzzle, very small nose leaf with smooth, triangular, short spear. Ears and tragus short, tragus with undulating, serrated contours. Forearm haired in its proximal third; coat colour deeply brown; hair on the head light at the basis, only hair tips dark. Extensive uropatagium with flat semicircular outer edge between long calcars. Calcar longer than foot. Distinctly developed tail (1/3 of uropatagial width); terminal with small stump projecting dorsally beyond the wing membrane.



Fig. 17: *Lichonycteris obscura*, head, tragus, and interfemoral membrane

Anoura

Small to mid-sized Glossophaginae with long thick fur. Long muzzle with small nose leaf; auricle and tragus short. Uropatagium sparsely developed, externally no tail visible (name!). Forearm proximally haired, coat colouring uniform with dark greyish brown to blackish brown.

A. caudifer (fig.18): Smallest species within this genus. Forearm length 35-38 mm, haired up to the half, coat very dark, almost black. Tragus carrying small protuberances at the outer margin. Uropatagium narrow with acute-angled fringe (semicircular in literature!), densely covered with hair on the dorsal side.



Fig. 18: *Anoura caudifer*, tragus and interfemoral membrane

A. cultrata: No data of my own referring to gross morphology.

A. geoffroyi (fig.19): Middle-sized, forearm length 40-44 mm. Contours of tragus smoothly rounded. Uropatagial fringe very narrow, with pointed parabolic contours (triangular Husson 1962). Forearm only hairy in its proximal third. Coat colour dark grey.



Fig. 19: *Anoura geoffroyi*, head, tragus, and interfemoral membrane

Hylonycteris

H. underwoodi: Very small glossophagine bat, forearm length 31-36 mm; externally resembling *Choeroniscus godmani*; no data of my own referring to outer morphology.

Scleronycteris

S. ega: No data of my own; forearm length about 35 mm.

Choeroniscus

Small to middle-sized flower bats with clearly stretched head; nose leaf very small, in frontal view equilaterally triangular. Short auricle with small tragus. Uropatagium large. The short tail remains embedded within the proximal third of the tail membrane. Calcar present, about the length of the foot. Pelage usually dark brown to blackish brown, colour mostly uniform, gradually turning into lighter shades ventrally and to darker ones dorsally. Hairs at the tip darker than at the basis, thus the "underwool" appears yellowish. Wing membranes dark brown.

C. godmani (fig.20): Very small bat, forearm length 32-34.8 mm. Head stretched, but less conspicuously than in the larger species of the genus. Tragus smooth. Metacarpalia: III>IV>V; 1. phalanges: III>IV>V. Plagiopatagium inserts at the tarsus. Coat dark brown to blackish brown.

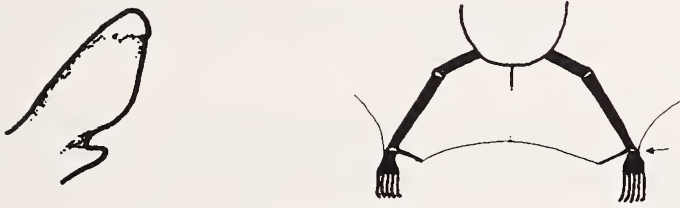


Fig. 20: *Choeroniscus godmani*, tragus and interfemoral membrane

C. minor (fig.21): Forearm length 35-36 mm. Tragus "granular" at the tip. Metacarpalia: III>IV>V; 1. phalanges: III>IV>V. Plagiopatagium as in *C. intermedius*. Coat colouring dark grey brown. Hairs darker at the tip than in the basal 3/4 of the shaft; thus the lower hair layer appears yellowish brown.



Fig.21: *Choeroniscus minor*, head and tragus

C. intermedius: Forearm length 34-36 mm. Metacarpalia: III>IV>V; 1. phalanges: III>IV>V. Plagiopatagium inserts at the proximal metatarsus.



Fig.22: *Choeroniscus intermedius*, interfemoral membrane

C. periosus: Largest species of the genus. Forearm length 40.4 mm. No data of my own referring to gross morphology.

Choeronycteris

C. mexicana (fig.22): Middle-sized microchiropteran (as a nectar feeder quite large) with distinctly elongated muzzle. Nose leaf and auricles small, short ears (rounded-triangular and in dorsal view looking like dolphin flippers). Small tragus, with its basis merely profiled.



Fig. 23: *Choeronycteris mexicana*, head, tragus, and interfemoral membrane

Forearm length 42-47 mm. Metacarpalia and 1. phalanx III>IV>V. Plagiopatagium inserts at the tarsus, uropatagium present, entirely including the short tail (only first third of the tail membrane). Calcar strong and straight, about same size as foot.

Pelage brownish grey to brown, ventrally brightened. Hairs only dark at the distal tip, the shaft is light. Wing membranes brown, but not as dark as in *Choeroniscus*.



Fig.24: *Choeronycteris harrisoni*, head

C. harrisoni (fig.23): Quite large blossom feeding bat with conspicuous, extremely long muzzle. Forearm length 40-43 mm. In other respect resembling *C. mexicana*.

Skull morphology

Differing from other mammals the chiropteran skull bones are delicate in order to reduce weight for flight capability. In adult animals the individual bones are mostly fused together leaving the sutures essential for bone discrimination not to be recognized. So, for proper orientation, it is certainly useful to refer to the juvenile skull yet lacking obliterations.

Within the chiroptera, the highly variable skull of phyllostomids is characterized by the following features:

Postorbital process lacking; the posterior rim of the orbita is, if at all, distinguishable only by lateral convexities of the frontalia.

Premaxillaria are completely present. Both the nasal and the palatal parts of the premaxillaries are completely developed and in adult individuals they are tightly connected to each other and to the maxillaria. Both palatine bones mark the boundary of two Foramina palatinae laterally.

The perioticum is largely separated from the rest of the skull (well visible in basal view). There are no more than 34 teeth:

- 2 3 1 - - 3 4 5 6 7
1 2 - 1 - 2 3 4 5 6 7

Sometimes, however, the number is reduced, down to 26:

- 2 3 1 - - 3 4 5 6 -
- - - 1 - 2 3 4 5 6 -

There are no more than two incisivi on each side of a jaw, the canini being always well developed. In the upper jaw only the genus *Anoura* bears three premolars, usually only two of them are present in one jaw side (P^3 and P^4); in most cases, the mandible bears only three premolars per half (P_2 , P_3 , P_4). If the premolars are limited to two, it is always P_2 which is missing. Considerable modifications predominantly affect the molar teeth (crown morphology); when the number is reduced, always M_3 is missing.

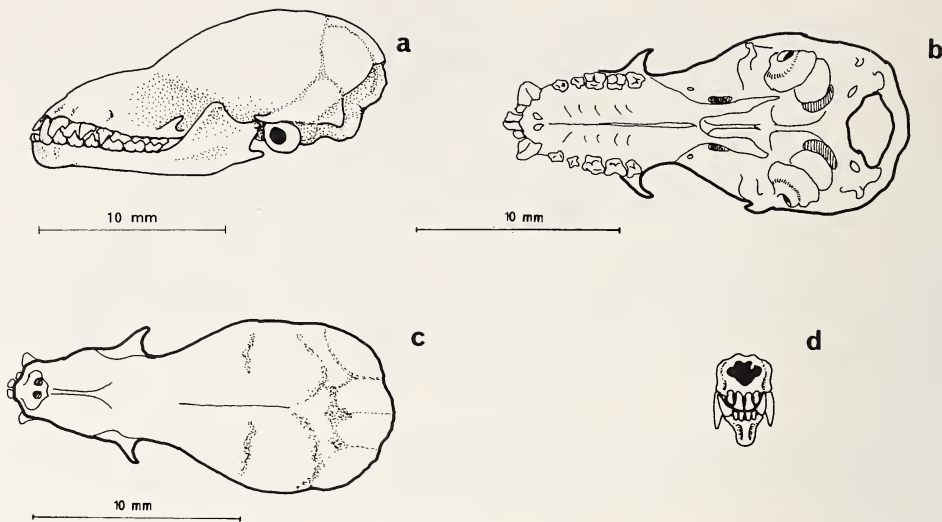


Fig.25: *Lionycteris spurrelli*, skull a: lateral view, b: basal view, c: dorsal view, d: frontal view

Skull descriptions of the single genera

Lionycteris (fig.25)

L. spurrelli: Skull: rostrum relatively short, approximately limited to one third of total length; distally flat and tapering. In lateral view, the upper incisivi continue the outline straightly.

In basal view the palate is pointedly trapezoid, width over the last molars considerably exceeds the distance of the canini to each other. Choanae situated quite anterior with the palate reaching only half the basal length. Praesphenoid outlined but without ridge, basisphenoid with strong convexities (basisphenoid pits). Pterygoids with hamuli ending shortly and pointedly, no pterygoid wings. No zygomatic arches.

Teeth: dental formula

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| - | 2 | 3 | 1 | - | - | 3 | 4 | 5 | 6 | 7 |
| 1 | 2 | - | 1 | - | 2 | 3 | 4 | 5 | 6 | 7 |

Incisivi present in the upper and lower jaw; the upper ones being orientated anteriorly, inner incisivi considerably larger than outer ones, long and spatular, with smooth edge, the outer ones only one third the size, pointedly trapezoid ("tomahawk"), producing an oblique edge which complements with those of the inner incisivi to an edge formed like a horseshoe.

Canini strong, with cingulum. Premolars caniniform, anterior premolar separated from canine tooth by distinct diastema. Molar teeth quite strong with broad crowns and dilambdodont ectoloph; anterior molar larger than the middle one, the posterior one being the smallest. Lower incisivi of same size, forming a closed row between the canini.

Lonchophylla (figs. 26-28)

Skull: similar to *Lionycteris*; in smaller forms the rostrum is distinctly less than half of the total skull length, in larger species almost half of it. Skull laterally stretched, only weak

lacrimal inflation. Zygomatic arches lacking in all species. Basisphenoid more or less arched, skull base almost at the same level as palate (in German literature: orthocran).

Teeth: dental formula

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| - | 2 | 3 | 1 | - | - | 3 | 4 | 5 | 6 | 7 |
| 1 | 2 | - | 1 | - | 2 | 3 | 4 | 5 | 6 | 7 |

both in the upper and in the lower jaw two pairs of incisivi present; upper incisors similar to *Lionycteris* ($I1 > I2$), the lower ones equal in size, with trifid edge, the width of a small gap between I2 and lower canine tooth corresponds to the crown width of the I2. Premolars with three cusps (not monocuspid as in *Lionycteris*). Anterior premolar separated from caninus by a diastema of its own length. Molar teeth still with functional masticatory surfaces.

L. thomasi: Posterior palate edge V-shaped; incisors and anterior edge of the premaxillaria in top view flat and almost straight. Basisphenoid pits vaulted. Palate length less than half the total length of skull. Last upper premolar with lingual cusp, giving the tooth a T-shaped appearance from top view. Anterior lower premolar with posterior (hooked) cusp.

L. mordax (fig.26): Posterior palate edge U-shaped; incisors and front edge of the premaxillaria pointed anteriorly in top view. Basisphenoid with deeply vaulted pits. Palate approximately half the total skull length. Last upper premolar without lingual cusp, thus appearing narrow from above. Anterior lower premolar without posterior cusp.

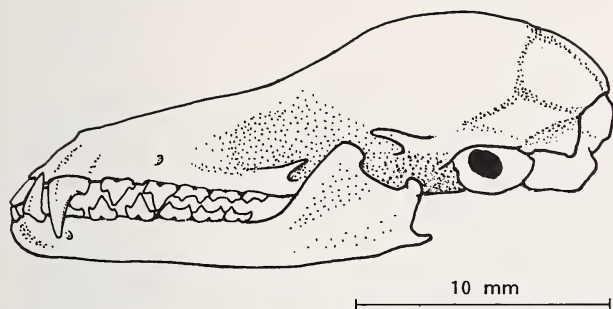


Fig.26: *Lonchophylla mordax*, skull lateral view

L. robusta (fig.27): Posterior margin of the palate U-shaped; anterior edge of the premaxillaria similar to *L. thomasi*, but a little more pointed. Basisphenoid only flatly vaulted. Palate approximately half the total skull length. Last upper premolar with a well developed lingual cusp, thus appearing triangular in top view. Anterior lower premolar with well developed hooked posterior cusp.

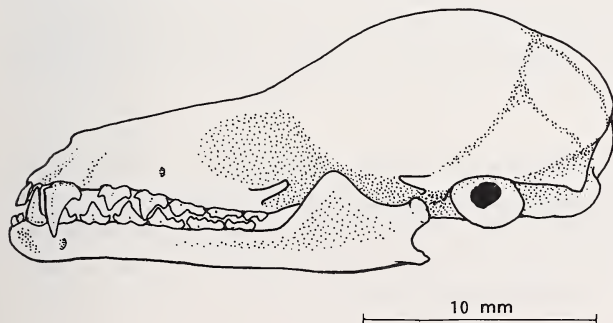


Fig.27: *Lonchophylla robusta*, skull lateral view

L. handleyi (fig.28): Like *L. robusta*, but the palate length clearly exceeds half the total skull length. Last upper premolar with insignificant lingual cusp; the posterior cusp of the anterior lower premolars is present and hooked.

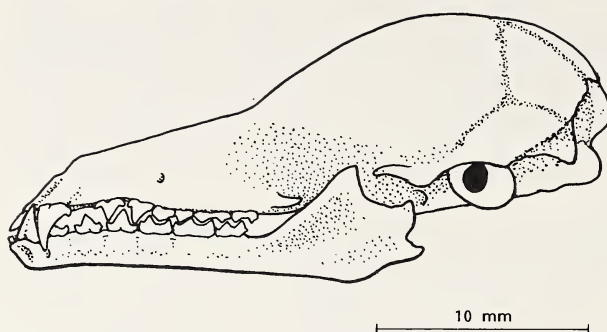


Fig.28: *Lonchophylla handleyi*, skull lateral view

Platalina (fig.29)

P. genoensium: Skull similar to *Lonchophylla*, very long rostrum, almost half the total skull length; transition premaxillaria to nasalia as well as of nasalia to frontalia very flat in lateral view (generic name). Zygomatic arches lacking; braincase flat, pterygoids do not reach the Bullae tympanicae.



Fig.29: *Platalina genoensium*, skull lateral view

Teeth: dental formula

- 2 3 1 - - 3 4 5 6 7
1 2 - 1 - 2 3 4 5 6 7

Inner upper incisivi strong, broad spatula form (frontal view), flat directed anteriorly; in lateral view, the incisors run out along the prolonged premaxillaria (the name *Platalina* also refers to the arrangement of the upper incisivi, which continue the flat line of outer contours of skull seen in lateral view). Lower incisivi present, with trifid edge. Canini strong, premolars with long narrow base, all postcanine teeth separated by wide gaps. Molar teeth narrow, without W-shaped ectoloph; triangular with simplified tricuspid pattern. Crowns in top view shorter than those of the premolars.

Brachyphylla (fig.30)

Skull: rostrum relatively short, braincase > viscerocranium. Solid zygomatic arches; length of palate < half the total skull length, posterior edge of the palate V-shaped with normally developed hamuli. Base moderately vaulted; strong joint processes (Proc. glenoidales).

Teeth: dental formula

- 2 3 1 - - 3 4 5 6 7
1 2 - 1 - - 3 4 5 6 7

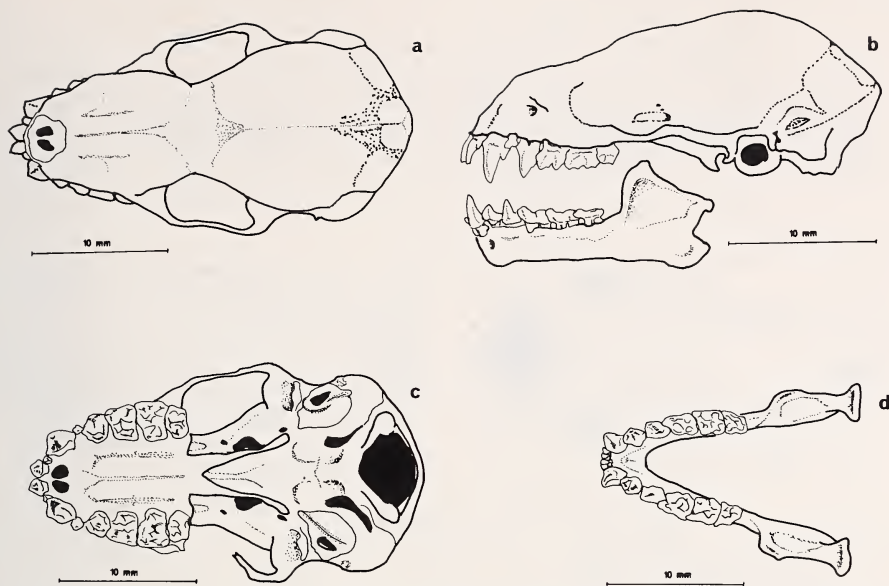


Fig.30: *Brachyphylla nana*, a: skull dorsal view, b: skull lateral view, c: skull basal view, d: mandible top view

Inner upper incisivi invigorates with pointed edge, outer incisors very small "squeezed into the gap between the large incisivi and the canine tooth"; caninus strong but only slightly longer than incisivi, anterior upper premolar very small, closely adjacent to canine tooth and to posterior premolars. Posterior premolar very strong, pointed and almost the same size as canine tooth. Upper molars broad with multiple cusps, lacking dilambdodont ectolophs (dentition of a fruit eater). Lower incisivi small, the inner ones equal in size to the outer ones, completely filling the gap between the canine teeth; lower premolars approximately equal in size with a pointed cusp (caniniform); last lower molar tooth narrower than the front molars; thus the outline of the tooth row becomes convex.

B. nana: Total skull length 27-29 mm.

B. cavernarum: Total skull length 30-32 mm.

Erophylla (figs.31-32)

Skull: rostrum moderately elongate; zygomatic arches present; palates with two distinct crosswise ridges anterior to each of the pterygoids; posterior edge of palate sharpened in a V-shaped way. Base initially flat at the choanae, but basisphenoid with well vaulted "basisphenoid pits". Mandibula in lateral view flat and straight, with flat coronoid process and strong angular process.

Teeth: dental formula

- 2 3 1 - - 3 4 5 6 7

1 2 - 1 - - 3 4 5 6 7

Upper incisivi: inner ones larger than outer ones; inner ones divided by a distinct middle gap, at the upper edge broader than at the root, crowns with comb-like edge ("ravioli edge"). Canines broad and strong; second upper premolar double the size of the first one, both with a broad crown. First upper molar almost double as long as broad, the outer edge

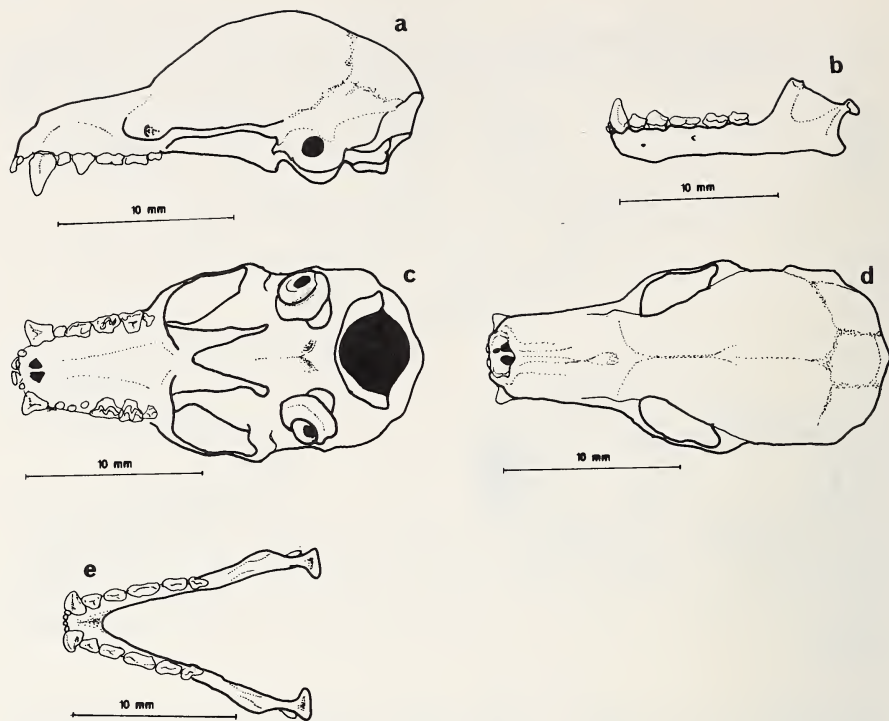


Fig.31: *Erophylla bombifrons*, a: skull lateral view, b: mandible lateral view, c: skull basal view, d: skull dorsal view, e: mandible top view

(buccal) flat and straight. The second upper molar is in basal view almost triangular, showing an incision at the outer edge. Third upper molar small, triangular with smooth outer edge. Lower incisivi small, about the same size and forming a continuous line between the broad canines. Second lower premolar slightly larger than the first; lower molars with flat crowns and sharp outer edge.

E. sezekorni: In lateral view, the skull shows a slightly concave transition from rostrum to braincase (fig.32).

E. bombifrons: Abrupt transition from rostrum to neurocranium with a distinct indentation at the suture separating the nasalia and frontalia (in lateral view). Behind, the cranium rises abruptly; the braincase being vaulted beginning from the root of the nose (fig.32).

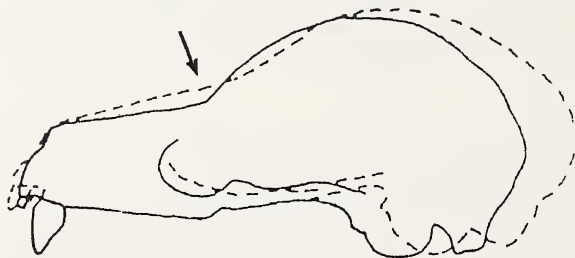


Fig.32: Skull contours of *E. bombifrons* (continuous line) and *E. sezekorni* (dotted line) adapted from Buden (1976)

Phyllonycteris (fig.33)

P. poeyi: Skull more elongate and flat; rostrum moderately elongate; continuous transition to the cranium in lateral view. Zygomatic arches lacking in the specimens examined. Palatal area slightly lowered against skull base (in German literature: klinorhynch). Premaxillaria shifted anteriorly, Foramina palatina minora lying in front of the canine alveoli.

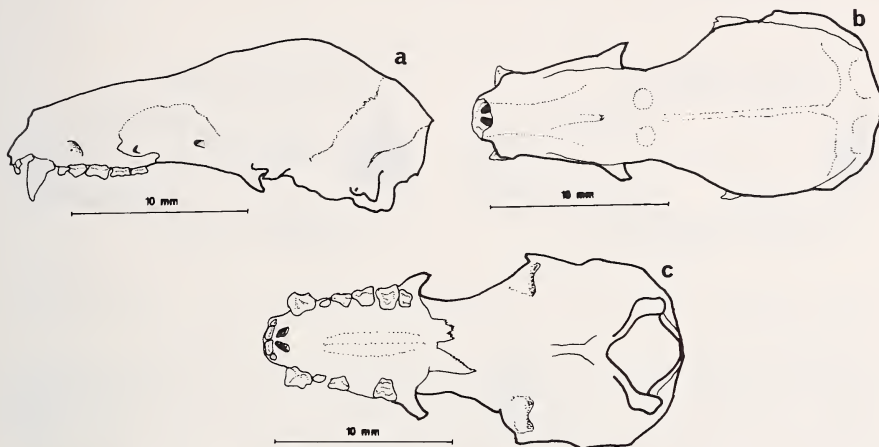


Fig.33: *Phyllonycteris poeyi*, skull a: lateral view, b: dorsal view, c: basal view

Teeth: dental formula

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| - | 2 | 3 | 1 | - | - | 3 | 4 | 5 | 6 | 7 |
| 1 | 2 | - | 1 | - | - | 3 | 4 | 5 | 6 | 7 |

Upper incisivi separated from canine tooth by broad diastema; inner ones larger than outer ones, orientated posteriorly, jointly forming an almost straight edge (teeth somewhat horselike). Canini strong and broad; first upper premolar small, the second one at least double the size with lingual cusp. Upper molars flat with broad crowns lacking a dilambdodont ectoloph.

Glossophaga (fig.34)

Skull: braincase longer than rostrum (only in *G. longirostris* almost of the same length). Zygomatic arches developed quite well and preserved in most specimens. Skull base vaulted to different extent within the species. *G. commissarisi* is separated from *G. soricina* by contours of the presphenoid. Mandibula with flat coronoid and distinct mentum.

Teeth: dental formula

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| - | 2 | 3 | 1 | - | - | 3 | 4 | 5 | 6 | 7 |
| 1 | 2 | - | 1 | - | 2 | 3 | 4 | 5 | 6 | 7 |

Upper incisivi uniform, sometimes slightly projecting forward, forming an almost complete curve between the canini (gaps between the outer incisivi and the canine teeth narrower than width of the outer incisivus), the inner incisivus is broader than high with straight edge; the outer one is shorter, but thus with its edge in one level with the inner one. Lower incisivi well developed, completely filling the space between the canini, with flat crowns (width = height) and rounded to roundly rectangular profile. Strong canine teeth with weak cingulum, the upper ones with distinct anterior and posterior edge. Upper

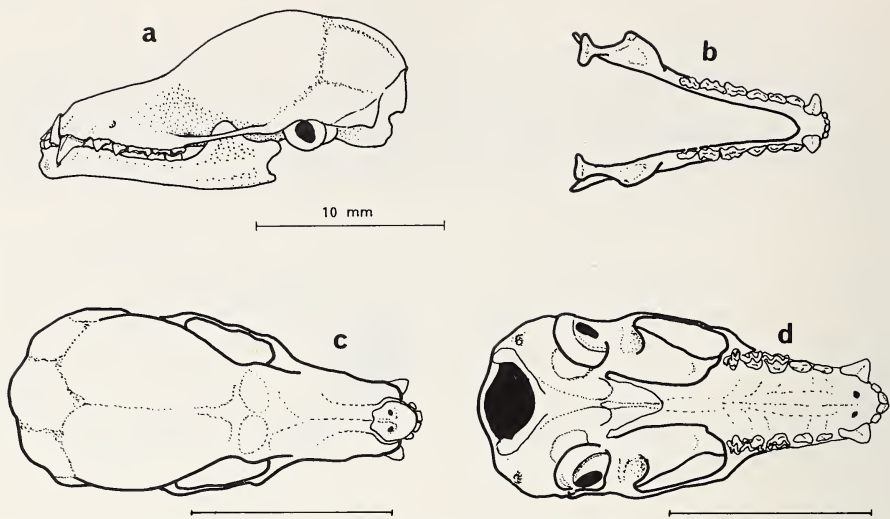


Fig.34: *Glossophaga commissarisi*, a: skull lateral view, b: mandible top view, c: skull dorsal view, d: skull basal view

premolars triangular in lateral view, with narrow cusps without styli. Upper molars with flattened W-pattern, third molar smaller than second, about half the surface of M2. The inside of all three molars with distinct convexities. The lower molars are of similar shape showing all five usual cusps, only the last molar slightly smaller.

G. soricina: Point of lower jaw with ridge on symphysis ("mentum"); pterygoids with lateral widenings ("pterygoid wings", but not the hamuli); presphenoid with distinct ridge; basisphenoid just slightly vaulted.

Upper incisivi projecting anteriorly, the inner ones larger than the outer ones, anterior edge of the premaxillare elongate (= in view from above incisivi well visible); lower incisivi contiguous and uniform in size.

G. commissarisi: Upper incisivi do not project forward, the inner ones about the same size as the outer ones, the anterior edge of the premaxillaria evenly rounded (incisivi in top view hardly visible); lower incisivi very small and comb-shaped; presphenoid ridge flattened, pterygoids lacking lateral widenings.

G. longirostris: Upper incisivi projecting anteriorly, the inner ones about the same size as the outer ones; lower incisivi large, forming a complete curve between the lower canini; symphyseal ridge (mentum) only weak, pterygoids bulging only to low extent.

G. leachii: Upper incisivi not projecting forward, the inner ones about the same size as the outer ones; anterior edge of the praemaxillare evenly rounded; complete presphenoid ridge present.

G. mexicana: Lower incisivi tiny, separated by distinct gaps, upper incisivi projecting anteriorly, the inner ones distinctly larger than the outer ones, anterior edge of the premaxillaria pointedly elongate. Pterygoid wings lacking, presphenoid ridge subterminally flattened.

Monophyllus (figs.35-36)

Skull: rostrum not quite half the total length of skull, skull appears more stretched than in *Glossophaga*, similar to *Anoura*.

Teeth: dental formula

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| - | 2 | 3 | 1 | - | - | 3 | 4 | 5 | 6 | 7 |
| 1 | 2 | - | 1 | - | 2 | 3 | 4 | 5 | 6 | 7 |

Teeth essentially like *Glossophaga*, the incisivi, however, remaining much smaller. The upper ones with distinct gaps between each other as well as to the canini and different in form: the inner ones with flat edge, the outer ones pointed. The lower incisivi are very small, with flat, rounded crowns, arranged in two pairs which are separated by a broad median gap.

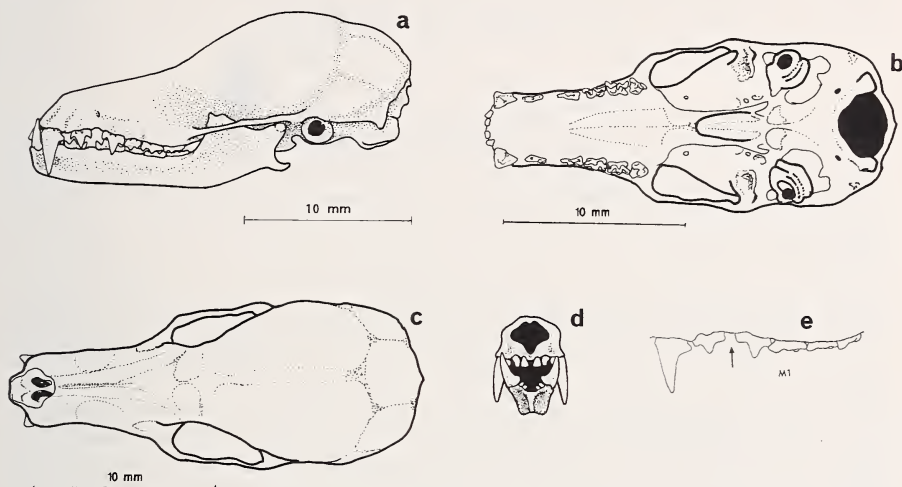


Fig.35: *Monophyllus redmani*, a: skull lateral view, b: skull basal view, c: skull dorsal view, d: incisivi, e: upper tooth row

M. redmani (fig.35): The upper premolars are separated from each other by a conspicuous gap, occupying more than half the crown length of the anterior upper premolar.

M. plethodon (fig.36): Upper premolars separated from each other just by a small diastema ($< 1/2$ the length of the anterior upper premolars).



Fig.36: *Monophyllus plethodon*, upper tooth row

Leptonycteris (fig.37)

L. nivalis: Skull long and flat, rostrum almost half of total length, braincase wider than high. Skull base well vaulted (basisphenoid), presphenoid ridge ending bulging; Pterygoid processes flat, slightly club-shaped (in contrast to *Choeroniscus*), Fossa mandibularis "shadowed" by Processus glenoidalis - i.e. comparatively solid mandibular joint.

Mandibula long and narrow, Processus coronoideus only slightly higher than Proc. articularis. Curvature of the Ramus mandibularis inserts yet caudal of the Proc. coronoideus.

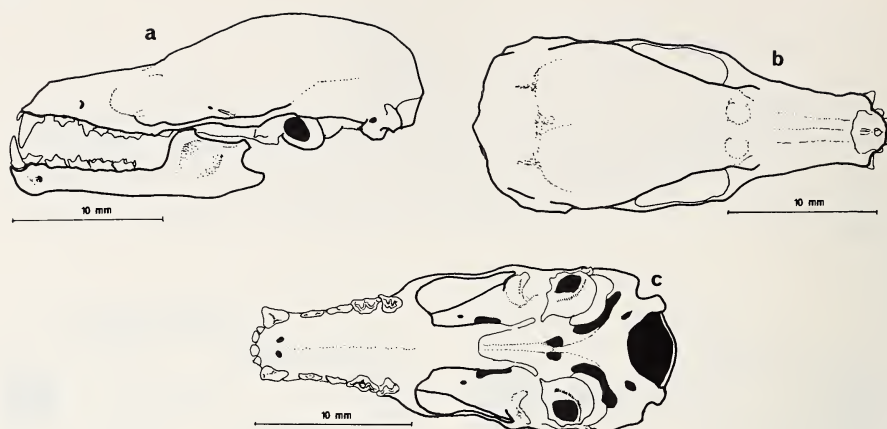


Fig.37: *Leptoncyteris nivalis*, a: skull lateral view, b: skull dorsal view, c: basal view

Teeth: dental formula
 - 2 3 1 - - 3 4 5 6 -
 1 2 - 1 - 2 3 4 5 6 -

Incisivi comparatively strong, forming a line, distance I^2 to C^1 longer than I^1 to I^2 . Lower incisivi of equal shape "droplet-spatula shape", the inner ones larger than the outer ones, medial separated by a diastema. Lower incisivi present, with low, flat, rounded crown. Well developed canini, the upper ones lacking a cingulum but with two secondary crowns, the one situated at the base of the main shaft being more conspicuous. Lower canini with distinct cingulum. Premolar teeth long and narrow with tall edges and distinct, but small styli. Seen from above, the anterior lower premolar (P_2) is vaulted outwards. Molars still with masticatory surface (W-Pattern) but already reduced, M_1 with very long narrow base.

Lichonycteris (fig.38)

L. obscura: Skull: braincase clearly longer than rostrum (comparatively short total length; cf. allometric data). Zygomatic arches very delicate and thus in most cases destroyed during preparation; skull base with presphenoid "ridge"; basisphenoid vaulted towards the basioccipitale.

Lower jaw with distinct mentum, Proc. coronoideus only slightly higher than articular process.

Teeth: dental formula
 - 2 3 1 - - 3 4 5 6 -
 - - - 1 - 2 3 4 5 6 -

Upper incisivi equally arranged between the canine teeth, showing gaps between the individual incisivi. Shape similar to *Choeroniscus* (I^1 droplet-spatula-shaped, I^2 dagger-

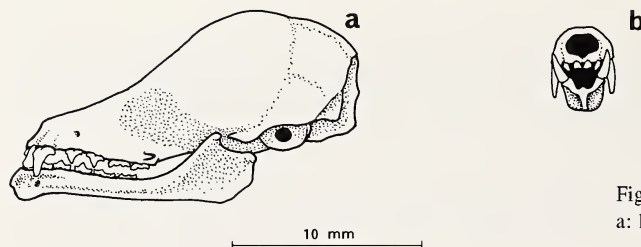


Fig.38: *Lichonycteris obscura*, a: lateral view, b: frontal view

shaped, pointed with flat outer base). Lower incisors missing. Canini simple, with a slight cingulum. Premolars comparatively short and wide, compared to other Glossophaginae. Upper molars without conceivable masticatory surface due to reduction of the commissurae.

Anoura (figs. 39-41)

A. caudifer (fig.39): Skull: rostrum not quite reaching half the total length of skull. Base moderately vaulted, no angular deviation between palatal and basal level (in German literature: orthocran). Choanae at about the same level with Fossa glenoidalis (palate comparatively long).

Teeth: dental formula

- 2 3 1 - 3 3 4 5 6 7
- - - 1 - 2 3 4 5 6 7

Upper incisors very small, the outer ones (dagger-shaped) twice the size of the inner ones (droplet-shaped), medially separated by wide gap (about four times the width of the incisivi). Anterior premolar very small and caniniform, clearly visible distance to canine tooth; also a diastema to the second premolar. Third upper premolar with three cusps, the second one more or less forming a two-cusped transitional form. Molars flat, but all three of them with functional masticatory surface (dilambdodont crown by top view). Row of teeth in basal view almost rectangular; width over canine teeth only slightly narrower than molar width of the palate. Lower incisivi missing; Proc. coronoideus very flat.

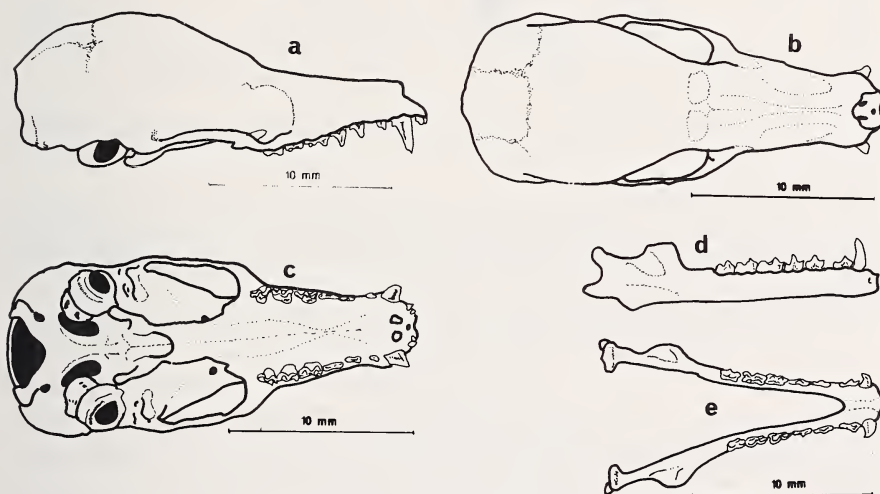


Fig.39: *Anoura caudifer*, a: skull lateral view, b: skull dorsal view, c: skull basal view, d: mandible lateral view, e: mandible top view

A. cultrata (fig.40): Similar to *A. caudifer*, but differences in dentition: upper canines strong with a sharp ridge running along the anterior edge; anterior lower premolar enlarged to a long, narrow blade.

A. geoffroyi (fig.41): Like *A. caudifer*, but considerably larger; last upper premolar with a median lingual cusp, projecting beyond the narrow base of the tooth.



Fig.40: *Anoura cultrata*,
mandible lateral view with P₂

A. latidens: Similar to *A. geoffroyi*, of about similar size; last upper premolar with a median lingual cusp, enclosed within the wide triangular base of the tooth.

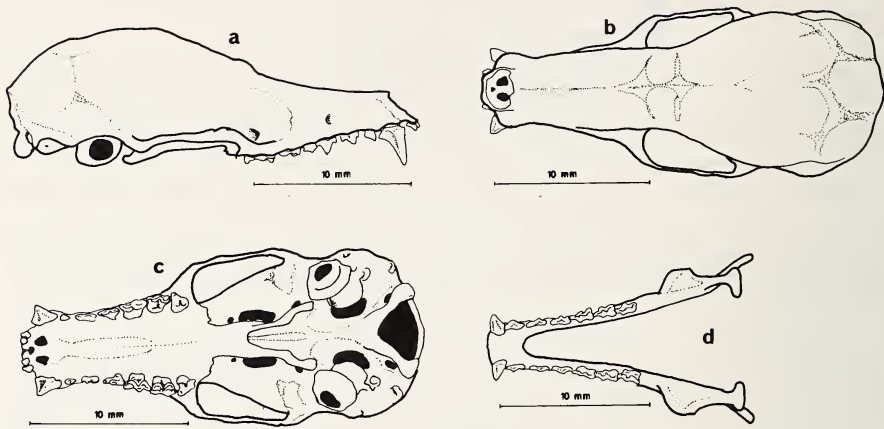


Fig.41: *Anoura geoffroyi*, a: skull lateral view, b: skull dorsal view, c: skull basal view, d: mandible top view

Scleronycteris (fig.42)

S. ega: Skull: due to incomplete specimen (Typus BMNH) no records on braincase; rostrum comparatively long (like *Choeroniscus* and *Hylonycteris*), no zygomatic arches preserved.

The pterygoid processes (hamuli) are short and do not reach the Bullae tympanicae.

Teeth: dental formula

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| - | 2 | 3 | 1 | - | - | 3 | 4 | 5 | 6 | 7 | |
| - | - | - | - | 1 | - | 2 | 3 | 4 | 5 | 6 | 7 |

Upper premolars with distinct distances from each other and from the canine tooth; molars in upper jaw with mesostyli, lower molar teeth only with just slightly narrowing crowns, too.

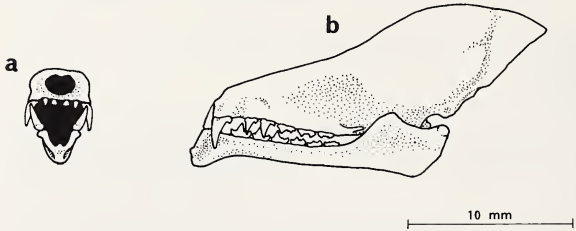


Fig.42: *Scleronycteris ega*,
a: skull frontal view, b: lateral
view (occiput missing)

Choëroniscus (figs. 43-45)

C. godmani (fig.43): Skull: rostrum long and narrow, but less than half the skull length. Braincase raised against rostrum, palatal area elevated against skull base (in German literature: airohynch). If the skull is placed on the palate plane, the highest point of the skull is not reached by the frontalia - as in the remaining glossophagines - but instead rather by the parietalia being separated by a distinct Fossa parietalis. Interorbital width hard to determine, as no postorbital processes visible. Foramen infraorbitale situated rostrad (within the anterior eighth of the total skull length, above the first upper premolar).

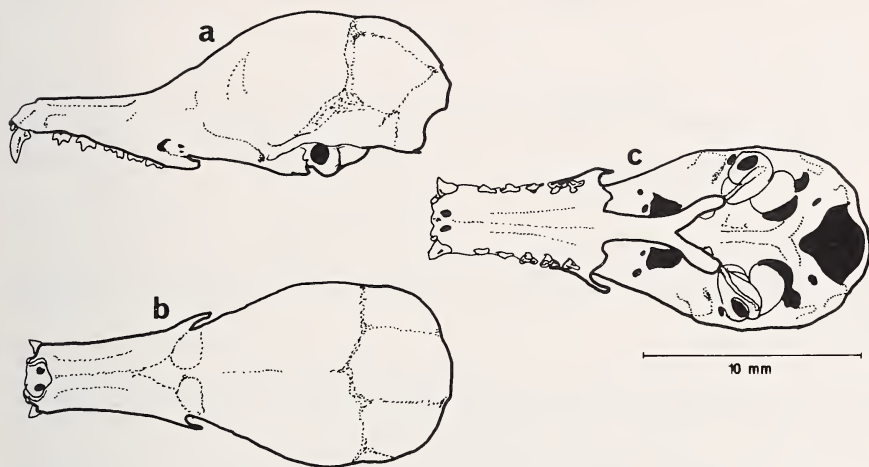


Fig.43: *Choëroniscus godmani* skull, a: lateral view, b: dorsal view, c: basal view

Skull base with conspicuously elongated rectangular palate surface (width over canini equals width over molars), roof of the palate almost reaching the Fossae mandibulares. Pterygoids form long, shovel-like widened processes coming in contact with the tympanohyoid bones at the bullae. Presphenoid smoothly adjoining the well vaulted basisphenoid. Contiguous ridge between presphenoid and basioccipitale comparatively broad, prolonged in two wings curving around the Foramen occipitale.

Teeth: dental formula

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| - | 2 | 3 | 1 | - | - | 3 | 4 | 5 | 6 | 7 |
| - | - | - | 1 | - | 2 | 3 | 4 | 5 | 6 | 7 |

Upper incisors very small, the outer ones being double the size of the inner ones, separated by a large medial diastema, very different in form: I^1 is flat, with stamp-shaped crown and definitely tiny. I^2 almost caniniform, but though of twice the size of I^1 so small that it does not match the height of the cingulum of the C^1 . Canines delicate and narrow with cingulum, length less than height of the maxillare at this level of the rostrum, separated from the anterior premolar (P^3 ; Miller 1907) by a large diastema. Premolars tricuspid, the middle conus being the highest, slightly exceeding cingulum C^1 . Base in basal view elongated and narrow. Molars almost lacking a masticatory surface. There is only a talon surrounding the hypoconus with the distal tip (metaconus) being the highest.

C. minor (fig.44): Skull with comparatively long rostrum, only slightly shorter than braincase; zygomatic arches very delicate, in most cases destroyed by preparation, but

visible in X-ray examination. Palate elongate, in basal view rectangular, similar to *C. godmani*, but considerably larger.

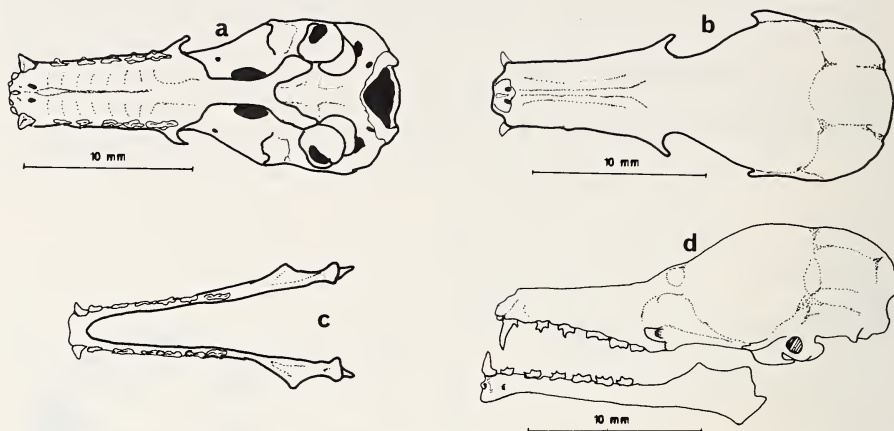


Fig.44: *Choeroniscus minor*, a: skull basal view, b: skull dorsal view, c: mandible top view, d: skull lateral view

Skull base characterized by conspicuously elongate pterygoid processes (hamuli), together with the tympanohyoideum reaching below the Bullae tympanicae. In connection with the alisphenoid they cover the vomer as well as one third of the presphenoid. Basisphenoid distinctly structured, with ridge development towards the basioccipitale, the latter parting into two wings which flank the Foramen magnum. Orbitae without distinguishable orbital processes - thus, in most cases, the interorbital width is no distinguishable measure from the postorbital width.

Palatal level elevated against skull base, in lateral view, the rostrum appears very straight. The contours of the braincase well vaulted, but without distinct indentation.

Mandibula elongate and narrow, lower incisivi missing - a median V-shaped notch between the canini, allowing the long tongue to pass without opening the mandible joint. Mentum with well developed symphyseal ridge; Proc. coronoideus flattened, merely projecting beyond the Proc. articularis. Angular process forms the proximal mandibular edge.

Teeth: dental formula

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| - | 2 | 3 | 1 | - | - | 3 | 4 | 5 | 6 | 7 |
| - | - | - | 1 | - | 2 | 3 | 4 | 5 | 6 | 7 |

Teeth very delicate showing wide gaps between individual premolars and molars. Premolars and molars tricuspid in lateral view lacking relevant masticatory surfaces. Incisivi only present in the upper jaw, very small, the outer ones exceeding the inner ones in size and grouped in two pairs by a wide medial gap. Canini thin and pointed with cingulum, premolars separated from the canini by distinctly developed diastema. Elongate, narrow base (without masticatory surface), protoconus about $\frac{3}{4}$ the height of the cingulum of the canini, metaconus higher than cingulum.

C. intermedius (fig.45): Like *C. minor*.

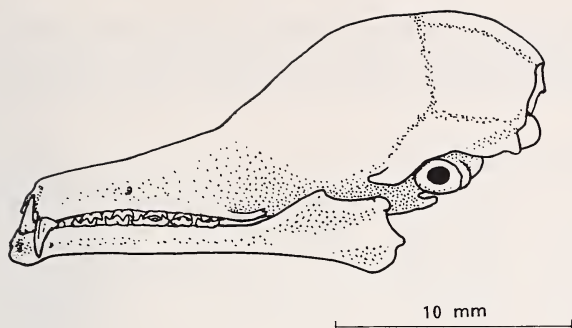


Fig. 45: *Choeroniscus intermedius*, skull lateral view

C. periosus: Similar to *C. minor*, but considerably larger. Clearly discernable from *Choeronycteris* by its lateral skull contours - lateral shape of the nose rather concave than convex.

Hylonycteris (fig. 46)

H. underwoodi: Skull: resembling *Choeroniscus* in most characteristics, but lacking the conspicuously elongated pterygoid processes. Pterygoids developed normally, as in almost all genera of this subfamily.

Ramus mandibularis stronger compared to *Choeroniscus*, with a more distinctly developed Proc. coronoideus (cf. data of coronoid height).

Teeth: dental formula

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| - | 2 | 3 | 1 | - | - | 3 | 4 | 5 | 6 | 7 |
| - | - | - | 1 | - | 2 | 3 | 4 | 5 | 6 | 7 |

The dental features of *Hylonycteris* correspond to those of *Choeroniscus*.

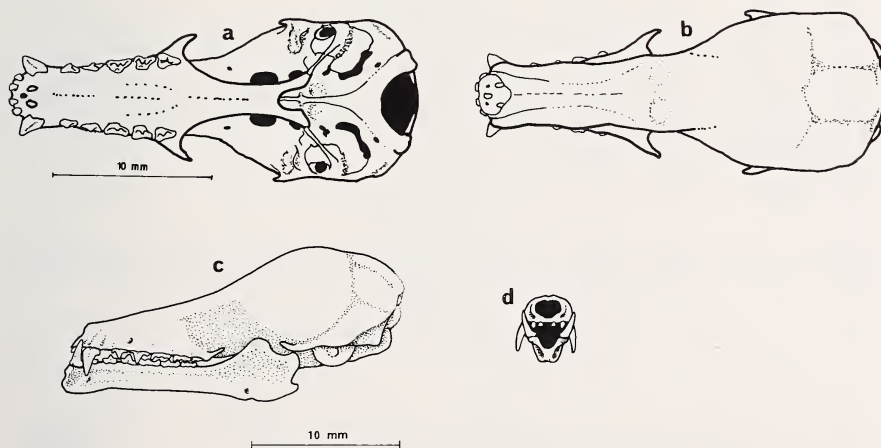


Fig. 46: *Hylonycteris underwoodi* skull, a: basal view, b: dorsal view, c: lateral view, d: frontal view

Choeronycteris (figs. 47-48)

C. mexicana (fig. 47): Skull: rostrum longer than braincase, in lateral view convex in its proximal third up to half the length, flat angle between the nasal and frontal (distinct

bend); orbital processes lacking; zygomatic arches highly reduced, usually undetectable at prepared skull. Skull base with elongate bony palate, the posterior edge reaching the alisphenoid canal. Palate trapezoid in basal view (caninal width of the palate smaller than molar width of the palate).

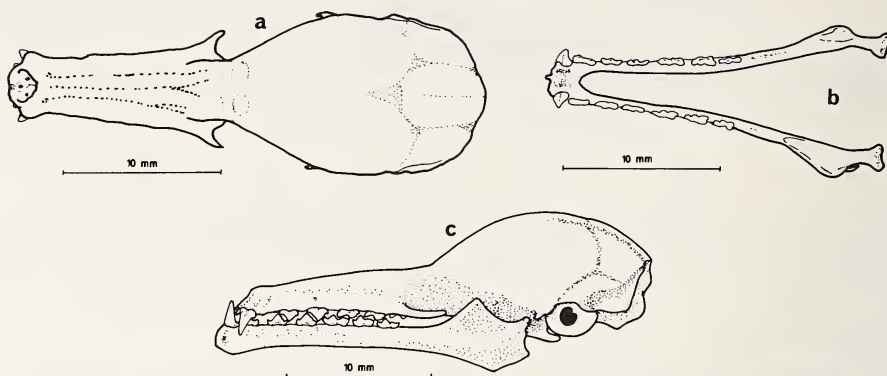


Fig.47: *Choeronycteris mexicana*, a: skull dorsal view, b: mandible top view, c: skull lateral view

Vomer covered by palatinum, septum continues as a presphenoid ridge up to the end of the presphenoid. Altogether, the base is stronger vaulted than in *Choeroniscus*. Pterygoids lead into elongate, shovel-like widened hamuli, diverging concavely and, together with the tympanohyale, forming a bony contact with the bullae.

Teeth: dental formula

| |
|-----------------------|
| - 2 3 1 - - 3 4 5 6 7 |
| - - - 1 - 2 3 4 5 6 7 |

Similar to *Choeroniscus*, but postcanine tooth row with larger interdental distances.

C. harrisoni (fig.48): Skull: like *C. mexicana*, but its rostrum is even more elongate. Thus both, the ridge of the nose and the mandibula, are still more convex and show a distinct angle to the braincase (lacrimal inflation). In basal view, the palate appears elongate-rectangular compared to *C. mexicana*.

Teeth: dental formula

| |
|-----------------------|
| - 2 3 1 - - 3 4 5 6 7 |
| - - - 1 - 2 3 4 5 6 7 |

Similar to *C. mexicana*, but the distances between the single teeth are even more distinctly; the last of the molars is situated far anterior of the mandibular joint.

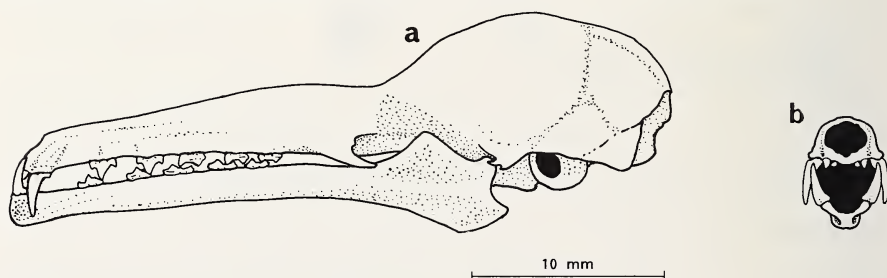


Fig.48: *Choeronycteris harrisoni* skull, a: lateral view, b: frontal view

Table 4a: Univariate analysis of skull measurements

SGL = total skull length, GL = length of palate, CH = coronoid process

N = sample size, MW = arithmetic mean, SD = standard deviation

| Species | SGL | | | GL | | | CH | | |
|-------------------------|-----|-------|------|----|-------|------|----|-------|------|
| | N | MW | SD | N | MW | SD | N | MW | SD |
| <i>P. hastatus</i> | 6 | 38.19 | 1.66 | 6 | 17.69 | 0.95 | 6 | 10.43 | 0.68 |
| <i>P. elongatus</i> | 5 | 29.98 | 0.74 | 5 | 13.43 | 0.30 | 5 | 7.07 | 0.51 |
| <i>C. perspicillata</i> | 20 | 23.15 | 0.76 | 18 | 10.71 | 0.40 | 10 | 5.37 | 0.19 |
| <i>C. castanea</i> | 2 | 19.55 | 0.08 | 2 | 8.75 | 0.44 | 2 | 3.96 | 0.03 |
| <i>C. subrufa</i> | 9 | 21.68 | 0.23 | 9 | 9.95 | 0.07 | 9 | 4.75 | 0.11 |
| <i>B. nana</i> | 7 | 28.38 | 0.64 | 7 | 11.57 | 0.35 | 6 | 6.99 | 0.27 |
| <i>B. cavernarum</i> | 4 | 30.88 | 0.43 | 4 | 14.09 | 0.26 | 4 | 8.39 | 0.30 |
| <i>E. sezekorni</i> | 15 | 24.58 | 0.64 | 15 | 10.78 | 0.37 | 14 | 4.39 | 0.30 |
| <i>E. bombifrons</i> | 13 | 24.38 | 0.45 | 13 | 11.12 | 0.37 | 12 | 4.47 | 0.25 |
| <i>P. poeyi</i> | 8 | 25.05 | 0.65 | 8 | 10.85 | 0.49 | 6 | 4.71 | 0.27 |
| <i>L. spurrelli</i> | 11 | 19.79 | 0.59 | 11 | 9.63 | 0.40 | 7 | 3.66 | 0.17 |
| <i>L. thomasi</i> | 14 | 20.92 | 0.43 | 14 | 12.12 | 0.69 | 5 | 3.42 | 0.13 |
| <i>L. mordax</i> | 7 | 23.62 | 0.49 | 7 | 12.83 | 0.72 | 5 | 4.18 | 0.17 |
| <i>L. robusta</i> | 11 | 26.09 | 0.44 | 11 | 14.49 | 0.28 | 8 | 4.39 | 0.14 |
| <i>L. handleyi</i> | 19 | 28.96 | 0.70 | 19 | 17.34 | 0.52 | 15 | 5.00 | 0.44 |
| <i>P. genovensium</i> | 2 | 32.35 | 0.50 | 2 | 19.11 | 0.20 | 2 | 22.68 | 0.18 |
| <i>G. soricina</i> | 38 | 20.90 | 0.68 | 35 | 11.46 | 0.51 | 14 | 3.61 | 0.28 |
| <i>G. commissarisi</i> | 8 | 20.24 | 0.39 | 8 | 10.76 | 0.43 | 5 | 3.71 | 0.30 |
| <i>G. longirostris</i> | 24 | 23.14 | 0.90 | 23 | 12.67 | 0.63 | 7 | 4.25 | 0.30 |
| <i>M. redmani</i> | 3 | 23.05 | 0.31 | 3 | 11.97 | 0.42 | 4 | 3.68 | 0.29 |
| <i>M. plethodon</i> | 5 | 23.25 | 0.66 | 5 | 11.68 | 0.77 | 4 | 4.00 | 0.31 |
| <i>A. caudifer</i> | 14 | 22.38 | 0.42 | 14 | 12.43 | 0.58 | 4 | 3.38 | 0.21 |
| <i>A. geoffroyi</i> | 17 | 25.53 | 0.51 | 17 | 14.11 | 0.64 | 6 | 4.43 | 0.37 |
| <i>A. brevirostrum</i> | 9 | 23.66 | 0.50 | 9 | 11.88 | 0.24 | 9 | 4.00 | 0.18 |
| <i>L. curasoae</i> | 8 | 27.91 | 0.30 | 8 | 16.09 | 0.39 | 2 | 4.83 | 0.38 |
| <i>L. nivalis</i> | 7 | 26.99 | 0.39 | 7 | 14.84 | 0.39 | 7 | 4.45 | 0.24 |
| <i>L. yerbabuenae</i> | 4 | 27.12 | 0.57 | 4 | 15.20 | 0.48 | 3 | 4.44 | 0.19 |
| <i>L. obscura</i> | 7 | 18.50 | 0.50 | 8 | 10.09 | 0.46 | 4 | 3.48 | 0.28 |
| <i>H. underwoodi</i> | 6 | 21.85 | 0.66 | 7 | 13.68 | 0.68 | 7 | 3.50 | 0.21 |
| <i>C. godmani</i> | 9 | 19.53 | 0.93 | 9 | 12.02 | 0.77 | 5 | 2.45 | 0.07 |
| <i>C. minor</i> | 11 | 22.78 | 0.74 | 11 | 14.99 | 1.18 | 5 | 3.05 | 0.20 |
| <i>C. indermedius</i> | 3 | 22.62 | 0.34 | 3 | 14.95 | 0.34 | | | |
| <i>C. inca</i> | 2 | 23.43 | 1.55 | 1 | 16.16 | | 2 | 3.07 | 0.16 |
| <i>C. mexicana</i> | 15 | 29.67 | 0.61 | 15 | 28.20 | 0.42 | 9 | 4.07 | 0.29 |
| <i>C. harrisoni</i> | 3 | 34.18 | 0.37 | 3 | 22.67 | 0.21 | 3 | 4.23 | 0.01 |
| <i>S. ega</i> | 1 | | | | | | 1 | 3.35 | |

Table 4b: Univariate analysis of skull measurements

OZR = upper tooth row, UKL = mandible length, CC = width over canini
N = sample size, MW arithmetic mean, SD = standard deviation

| Species | OZR | | | UKL | | | CC | | |
|-------------------------|-----|-------|------|-----|-------|------|----|------|------|
| | N | MW | SD | N | MW | SD | N | MW | SD |
| <i>P. hastatus</i> | 5 | 13.07 | 0.54 | 5 | 24.86 | 1.32 | 6 | 9.37 | 0.56 |
| <i>P. elongatus</i> | 5 | 10.63 | 0.35 | 5 | 19.15 | 0.23 | 5 | 7.23 | 0.39 |
| <i>C. perspicillata</i> | 20 | 7.74 | 0.30 | 20 | 14.23 | 0.69 | 20 | 4.75 | 0.29 |
| <i>C. castanea</i> | 2 | 6.32 | 0.11 | 2 | 12.01 | 0.27 | 2 | 4.20 | 0.17 |
| <i>C. subrufa</i> | 9 | 6.85 | 0.20 | 9 | 13.43 | 0.19 | 9 | 4.43 | 0.12 |
| <i>B. nana</i> | 7 | 9.44 | 0.20 | 7 | 18.13 | 0.40 | 7 | 6.10 | 0.24 |
| <i>B. cavernarum</i> | 4 | 10.77 | 0.38 | 4 | 20.69 | 0.39 | 4 | 6.59 | 0.22 |
| <i>E. sezekorni</i> | 15 | 7.89 | 0.26 | 15 | 15.65 | 0.57 | 15 | 4.90 | 0.28 |
| <i>E. bombifrons</i> | 13 | 7.85 | 0.20 | 13 | 51.61 | 0.33 | 13 | 5.16 | 0.30 |
| <i>P. poeyi</i> | 8 | 7.67 | 0.23 | 7 | 15.57 | 0.40 | 8 | 5.26 | 0.36 |
| <i>L. spurrelli</i> | 11 | 6.31 | 0.25 | 8 | 12.52 | 0.51 | 10 | 3.08 | 0.18 |
| <i>L. thomasi</i> | 14 | 6.67 | 0.28 | 12 | 13.82 | 0.53 | 14 | 3.55 | 0.16 |
| <i>L. mordax</i> | 6 | 7.99 | 0.21 | 5 | 15.82 | 0.24 | 6 | 3.56 | 0.19 |
| <i>L. robusta</i> | 11 | 9.54 | 0.33 | 10 | 17.60 | 0.49 | 11 | 3.85 | 0.14 |
| <i>L. handleyi</i> | 19 | 10.62 | 0.33 | 17 | 20.22 | 0.60 | 19 | 4.20 | 0.10 |
| <i>P. genovensium</i> | 2 | 10.49 | 0.22 | 2 | 22.68 | 0.18 | 2 | 4.26 | 0.22 |
| <i>G. soricina</i> | 36 | 7.18 | 0.26 | 36 | 13.61 | 0.47 | 36 | 3.70 | 0.27 |
| <i>G. commissarisi</i> | 8 | 6.89 | 0.15 | 7 | 13.20 | 0.47 | 7 | 3.75 | 0.10 |
| <i>G. longirostris</i> | 23 | 7.97 | 0.27 | 21 | 15.21 | 0.66 | 23 | 4.03 | 0.16 |
| <i>M. redmani</i> | 4 | 8.38 | 0.25 | 4 | 14.85 | 0.24 | 3 | 3.96 | 0.08 |
| <i>M. plethodon</i> | 5 | 8.17 | 0.24 | 5 | 14.66 | 0.46 | 5 | 4.06 | 0.44 |
| <i>A. caudifer</i> | 14 | 8.13 | 0.35 | 14 | 15.70 | 0.37 | 14 | 4.01 | 0.15 |
| <i>A. geoffroyi</i> | 16 | 9.57 | 0.22 | 17 | 17.89 | 0.54 | 17 | 4.57 | 0.24 |
| <i>A. brevirostrum</i> | 9 | 8.12 | 0.24 | 9 | 16.21 | 0.33 | 9 | 4.66 | 0.17 |
| <i>L. curasoeae</i> | 8 | 9.45 | 0.18 | 8 | 18.69 | 0.22 | 8 | 4.82 | 0.21 |
| <i>L. nivalis</i> | 8 | 8.84 | 0.18 | 8 | 18.31 | 0.37 | 6 | 4.44 | 0.15 |
| <i>L. yerbabuenae</i> | 4 | 8.83 | 0.25 | 4 | 18.28 | 0.32 | 4 | 4.44 | 0.43 |
| <i>L. obscura</i> | 8 | 5.87 | 0.28 | 6 | 12.48 | 0.46 | 7 | 3.28 | 0.16 |
| <i>H. underwoodi</i> | 7 | 7.60 | 0.49 | 7 | 14.93 | 0.70 | 7 | 3.43 | 0.13 |
| <i>C. godmani</i> | 8 | 6.95 | 0.39 | 7 | 13.81 | 0.52 | 8 | 3.11 | 0.29 |
| <i>C. minor</i> | 10 | 7.90 | 0.62 | 9 | 16.42 | 0.68 | 11 | 3.56 | 0.18 |
| <i>C. indermedius</i> | 3 | 7.87 | 0.05 | 3 | 15.90 | 0.61 | 3 | 3.63 | 0.15 |
| <i>C. inca</i> | 2 | 8.38 | 0.03 | 1 | 17.68 | | 2 | 3.62 | 0.52 |
| <i>C. mexicana</i> | 15 | 11.26 | 0.35 | 15 | 21.31 | 0.48 | 15 | 4.24 | 0.13 |
| <i>C. harrisoni</i> | 3 | 12.80 | 0.28 | 3 | 25.56 | 0.23 | 3 | 4.10 | 0.10 |
| <i>S. ega</i> | 1 | 7.44 | | 1 | 15.74 | | 1 | 3.84 | |

Morphometry

Univariate analysis

For the taxa examined the results of univariate analysis of some selected skull measures are given in tab.4a and 4b. The results show that the range of the data may overlap among individual species of a genus, even if the means differ from each other significantly.

Statistically, only those random samples comprising numerous individuals can be processed, whereas rare species with little material available may only be referred to by individual records.

Sex-specific differences

Within the genus *Phyllostomus* (examined as outgroup), in the extremely large species *P. hastatus*, most of the male skull measures examined rank over the female ones (see appendix).

In all species of the genus *Choeroniscus* the cranial length values of the females proved statistically significantly larger than those of the corresponding males ($p < 0.05$, t-test).

In *Lonchophylla robusta* the only available male was distinctly larger than the females examined - in contrast to the smaller species of the genus. In *L. handleyi* which is even larger, in 12 of 17 parameters the male values on average exceed the female ones, too, although in the given random samples this could not be secured statistically. In all the remaining taxa the sexes did not show any significant differences in their skull measures.

Skull proportions

The extent of adaptation to nectarivory may be expressed by the relation of rostrum length to total skull length, as the following measure relations give evidence:

- Total length of skull to length of palate.
- Total length of skull to upper tooth row.
- Height of braincase cranium to length of palate.
- Total skull length to coronoid height.
- Height of braincase cranium to coronoid height.
- Mandible length to coronoid height.

Total length of skull to length of palate: the quotient of the means for the total skull length (MWx) and the length of the bony palate (MWy) gives a good idea of relative muzzle length in the species examined (the larger the quotient, the shorter the palate) (tab.5, fig.49).

Table 5: Proportion of mean total skull length (MWx) / mean palate length (MWy)

| | x / y | SD | | x / y | SD |
|-----------------------|-------|------|-----------------------|-------|------|
| <i>Phyllonycteris</i> | 2.30 | 0.08 | <i>Anoura</i> | 1.83 | 0.07 |
| <i>Erophylla</i> | 2.24 | 0.07 | <i>Leptonycteris</i> | 1.77 | 0.05 |
| <i>Carollia</i> | 2.28 | 0.04 | <i>Lonchophylla</i> | 1.73 | 0.08 |
| <i>Lionycteris</i> | 2.08 | 0.04 | <i>Choeronycteris</i> | 1.61 | 0.05 |
| <i>Monophyllus</i> | 1.95 | 0.07 | <i>Hylonycteris</i> | 1.57 | 0.02 |
| <i>Glossophaga</i> | 1.83 | 0.06 | <i>Choeroniscus</i> | 1.57 | 0.08 |
| <i>Lichonycteris</i> | 1.83 | 0.07 | <i>Musonycteris</i> | 1.50 | - |

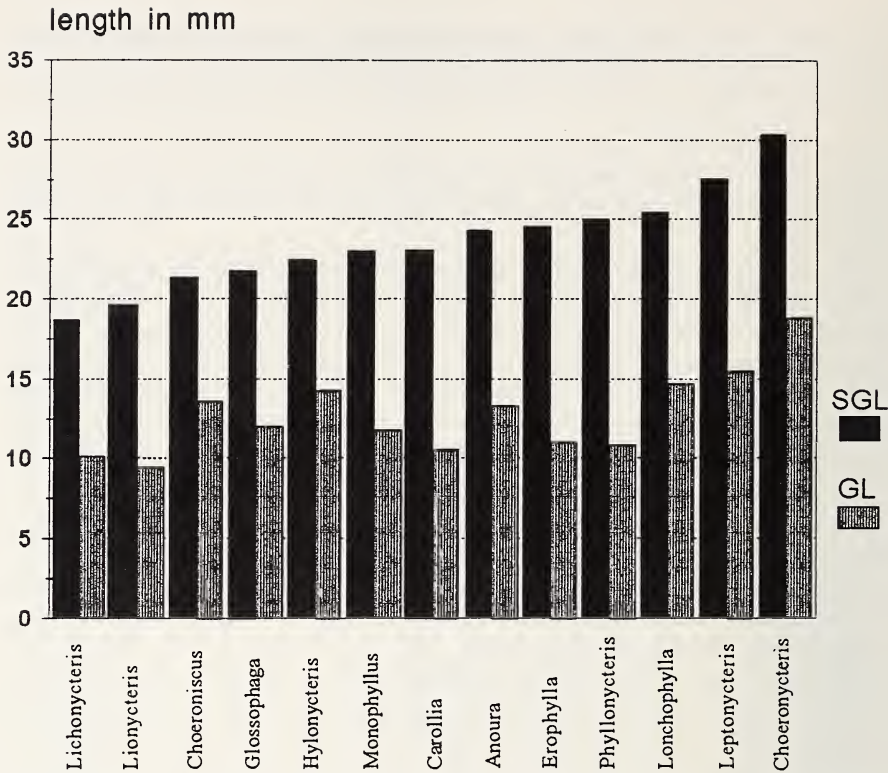


Fig.49: Skull proportions: total skull length (SGL) to palate (GL) of nectarivorous bat genera (arranged to absolute body size)

Total length of skull to upper tooth row: the length of the upper tooth row between caninus and last molar (MWy) is suitable as an additional measure for characterizing the muzzle length, especially useful in those species which show a V-shaped palate (i.e. *Erophylla*, *Brachyphylla*): tab.6.

Table 6: Proportion of mean total skull length (MWx) / mean length of the upper tooth row (MWy)

| | x / y | SD | | x / y | SD |
|----------------------|-------|------|-----------------------|-------|------|
| <i>Lionycteris</i> | 3.18 | 0.04 | <i>Platalina</i> | 2.81 | - |
| <i>Lichonycteris</i> | 3.15 | 0.12 | <i>Hylonycteris</i> | 2.81 | - |
| <i>Erophylla</i> | 3.11 | 0.06 | <i>Choeroniscus</i> | 2.80 | 0.08 |
| <i>Brachyphylla</i> | 2.99 | - | <i>Monophyllus</i> | 2.77 | 0.09 |
| <i>Carollia</i> | 2.98 | 0.08 | <i>Anoura</i> | 2.68 | 0.08 |
| <i>Leptonycteris</i> | 2.98 | 0.08 | <i>Choeronycteris</i> | 2.62 | 0.06 |
| <i>Glossophaga</i> | 2.93 | 0.06 | <i>Musonycteris</i> | 2.62 | - |
| <i>Lonchophylla</i> | 2.81 | 0.18 | | | |

Height of braincase to palate length: in order to compare measures being as independent as possible of each other, the height of the braincase (MWx) is related to the length of the palate (MWy): tab.7.

Table 7: Proportion of mean height of braincase (MWx) / mean length of palate (MWy)

| | x / y | SD | | x / y | SD |
|-----------------------|-------|------|-----------------------|-------|------|
| <i>Brachyphylla</i> | 0.96 | 0.05 | <i>Anoura</i> | 0.65 | 0.04 |
| <i>Carollia</i> | 0.94 | 0.06 | <i>Leptonycteris</i> | 0.59 | 0.02 |
| <i>Phyllonycteris</i> | 0.90 | 0.03 | <i>Lonchophylla</i> | 0.59 | 0.06 |
| <i>Erophylla</i> | 0.88 | 0.03 | <i>Choeroniscus</i> | 0.56 | 0.06 |
| <i>Phyllostomus</i> | 0.85 | - | <i>Hylonycteris</i> | 0.53 | - |
| <i>Lionycteris</i> | 0.82 | 0.02 | <i>Choeronycteris</i> | 0.50 | 0.02 |
| <i>Lichonycteris</i> | 0.74 | 0.03 | <i>Platalina</i> | 0.49 | - |
| <i>Monophyllus</i> | 0.69 | 0.05 | <i>Musonycteris</i> | 0.40 | - |
| <i>Glossophaga</i> | 0.69 | 0.04 | | | |

Total skull length to coronoid height: with relative size of the coronoid process, the force of the M. temporalis to move and hold the mandible against the upper jaw increases. Thus, coronoid height is a morphological indicator for masticatory pressure achieved by the contracting M. temporalis. The larger the Proc. coronoideus, the stronger the bite. With respect to a functional shift to nectar feeding, also the proportions of coronoid height (MWx) and total skull length (MWy) may be interesting: tab. 8.

Table 8: Proportion of mean coronoid height (MWx) / mean skull length (MWy)

| | x / y | SD | | x / y | SD |
|-----------------------|-------|------|-----------------------|-------|------|
| <i>Phyllostomus</i> | 0.25 | - | <i>Leptonycteris</i> | 0.16 | 0.01 |
| <i>Brachyphylla</i> | 0.25 | - | <i>Anoura</i> | 0.16 | 0.35 |
| <i>Phyllonycteris</i> | 0.19 | 0.01 | <i>Monophyllus</i> | 0.16 | 0.01 |
| <i>Erophylla</i> | 0.18 | 0.01 | <i>Platalina</i> | 0.16 | - |
| <i>Lionycteris</i> | 0.18 | 0.01 | <i>Hylonycteris</i> | 0.16 | - |
| <i>Lichonycteris</i> | 0.18 | 0.02 | <i>Choeronycteris</i> | 0.14 | 0.01 |
| <i>Glossophaga</i> | 0.18 | 0.01 | <i>Choeroniscus</i> | 0.13 | 0.01 |
| <i>Lonchophylla</i> | 0.17 | 0.01 | <i>Musonycteris</i> | 0.12 | - |

Height of braincase to coronoid height: to obtain a measure for the functional reduction of the jaw apparatus, apart from the relationship to total length it may also be useful to compare a quantity independent of rostrum prolongation, e.g. braincase height (MWx) with coronoid height (MWy), as with increasing jaw length the coronoid process does not necessarily grow at the same ratio. Only if a Crista sagittalis is present, the height of the braincase gives evidence of a functional relation to the Ramus mandibularis. Otherwise, this measure is affected essentially by the current morphology (and volume) of the brain (tab. 9).

Table 9: Proportion of mean height of braincase (MWx) / mean coronoid length (MWy)

| | x / y | SD | | x / y | SD |
|----------------------|-------|------|-----------------------|-------|------|
| <i>Brachyphylla</i> | 1.57 | - | <i>Glossophaga</i> | 2.14 | 0.19 |
| <i>Phyllostomus</i> | 1.59 | - | <i>Phyllonycteris</i> | 2.14 | 0.11 |
| <i>Platalina</i> | 1.76 | - | <i>Musonycteris</i> | 2.16 | - |
| <i>Lonchophylla</i> | 1.87 | 0.19 | <i>Erophylla</i> | 2.17 | 0.13 |
| <i>Carollia</i> | 1.87 | 0.18 | <i>Monophyllus</i> | 2.17 | 0.13 |
| <i>Leptonycteris</i> | 1.99 | 0.11 | <i>Lichonycteris</i> | 2.20 | 0.19 |
| <i>Hylonycteris</i> | 2.12 | - | <i>Choeronycteris</i> | 2.27 | 0.17 |
| <i>Lionycteris</i> | 2.13 | 0.07 | <i>Choeroniscus</i> | 2.80 | 0.28 |
| <i>Anoura</i> | 2.13 | 0.25 | | | |

Mandible length to coronoid height: as a reliable measure for rostrum length the length of the mandible may be quoted. Relating mandibular length (MWx) to coronoid height (MWy), the quotients appear in the following distribution: tab.10.

Table 10: Proportion of mean mandibula length (MWx) / mean coronoid heigth (MWy)

| | x / y | SD | | x / y | SD |
|-----------------------|-------|------|-----------------------|-------|------|
| <i>Carollia</i> | 2.77 | 0.14 | <i>Platalina</i> | 4.22 | - |
| <i>Phyllonycteris</i> | 3.35 | 0.20 | <i>Hylonycteris</i> | 4.24 | - |
| <i>Lionycteris</i> | 3.40 | 0.13 | <i>Anoura</i> | 4.25 | 0.39 |
| <i>Erophylla</i> | 3.52 | 0.18 | <i>Scleronycteris</i> | 4.70 | - |
| <i>Glossophaga</i> | 3.62 | 0.20 | <i>Choeronycteris</i> | 5.26 | 0.32 |
| <i>Lonchophylla</i> | 3.93 | 0.19 | <i>Choeroniscus</i> | 5.49 | 0.28 |
| <i>Leptonycteris</i> | 4.05 | 0.27 | <i>Musonycteris</i> | 6.01 | - |
| <i>Monophyllus</i> | 4.08 | 0.24 | | | |

These quotients clearly reflect different levels of specialization within the group but do not necessarily allow statements on the construction principles they are based on. Although size differences within nectar feeding bats are moderate, size-dependent shifts in proportion cannot be definitely ruled out. After all, forearm length between *Lichonycteris obscura* (30.3 mm) and *Leptonycteris nivalis* (58.2 mm) differs by approximately 100 percent.

So, the allometric relations between the measures mentioned within the subfamily and the neighbouring phyllostomid genera *Carollia* (Carollinae) and *Phyllostomus* (Phyllostominae) will be referred to.

Allometrics

Allometric comparison of individual genera

In this study, a large portion of the species to be examined was represented by very few individuals. Some of them show an intraspecific variability proving larger than interspecific distances. Furthermore, measured differences sometimes are within the error range pre-determined by the methods of measuring. Thus, a comprehensive comparison of intraspecific allometries for the entire group may be impossible, and any examination will

have to be restricted to intra- and intergeneric allometries. These, however, are quite suitable to give evidence of structural morphologic peculiarities and systematic relations in different genera.

Regression (represented by the reduced major axis) was calculated with reference to the measure SIZE for the following skull measures:

- Width over canini (CC)
- Upper tooth row (OZR)
- Length of palate (GL)
- Mandible length (UKL)
- Coronoid height (CH)

The formulae are given in detail in Rempe (1962).

The following tabular summaries show arithmetic mean values of both parameters as logarithms, the gradient ($\tan \alpha$) of the reduced major axis in a double logarithmic system of coordinates, the correlation coefficient (r) and the distance of the log. mean value to the reduced major axis of the outgroup ("Lot") for each genus examined (tab.11-15). In the graphs the reduced major axis for the outgroup (*Carollia* and *Phyllostomus* calculated as a unified common sample) is drawn as a broken line. The coordinate resulting from the mean values for both parameters is marked as a point. In case the correlation can be secured by the size of the random sample, the reduced major axis of the respective nectarivorous genus is represented as a straight line scoring the coordinates of the mean value (fig.50-54).

The generic names are placed aside to the mean value coordinates (An = *Anoura*, Bp = *Brachyphylla*, Ca = *Carollia*, Cs = *Choeroniscus*, Ct = *Choeronycteris*, Ep = *Erophylla*, Gp = *Glossophaga*, Hn = *Hylonycteris*, Lc = *Lichonycteris*, Le = *Leptonycteris*, Li = *Lionycteris*, Ps = *Phyllostomus*, Pn = *Phyllonycteris*, Lp = *Lonchophylla*, Mp = *Monophyllus*, Ms = *Musonycteris* (*C. harrisoni*), Pn = *Phyllonycteris*, Ps = *Phyllostomus*, Pt = *Platalina*).

A synopsis of the calculated distances to the outgroup is given in tab.16. Diagrams with individual values and - if available - distribution ellipses for each genus do exist and can be ordered from the author.

Table 11: Allometric proportions: width over canini to SIZE

| | MW SIZE | MW CC | $\tan \alpha$ | r | Lot |
|-----------------------|---------|--------|---------------|--------|--------|
| <i>Carollia</i> | 3.0448 | 0.6640 | 0.5384 | 0.7832 | 0.0043 |
| <i>Phyllostomus</i> | 3.4483 | 0.8966 | 0.4093 | 0.9364 | 0.0016 |
| <i>Brachyphylla</i> | 3.3195 | 0.7942 | | | 0.0306 |
| <i>Erophylla</i> | 3.1089 | 0.7045 | | | 0.0003 |
| <i>Phyllonycteris</i> | 3.1374 | 0.7200 | | | 0.0010 |
| <i>Lionycteris</i> | 2.8499 | 0.4884 | 0.8913 | 0.6971 | 0.0688 |
| <i>Lonchophylla</i> | 3.0317 | 0.5811 | 0.2907 | 0.8792 | 0.0797 |
| <i>Platalina</i> | 3.2137 | 0.6286 | | | 0.1359 |
| <i>Glossophaga</i> | 2.9211 | 0.5785 | | | 0.0193 |
| <i>Monophyllus</i> | 2.9833 | 0.6050 | | | 0.0282 |
| <i>Lichonycteris</i> | 2.8387 | 0.5154 | | | 0.0354 |
| <i>Leptonycteris</i> | 3.1805 | 0.6629 | 1.4206 | 0.7664 | 0.0827 |
| <i>Anoura</i> | 3.0543 | 0.6396 | 0.6239 | 0.7455 | 0.0341 |
| <i>Choeromiscus</i> | 2.9186 | 0.5364 | 0.5709 | 0.8843 | 0.0600 |
| <i>Hylonycteris</i> | 2.9045 | 0.5347 | 0.7449 | 0.7511 | 0.0536 |
| <i>Choeronycteris</i> | 3.1753 | 0.6253 | | | 0.1173 |
| <i>Musonycteris</i> | 3.2070 | | | | 0.7607 |
| Outgroup | 3.1540 | 0.7305 | 0.5698 | 0.6900 | 0.0000 |

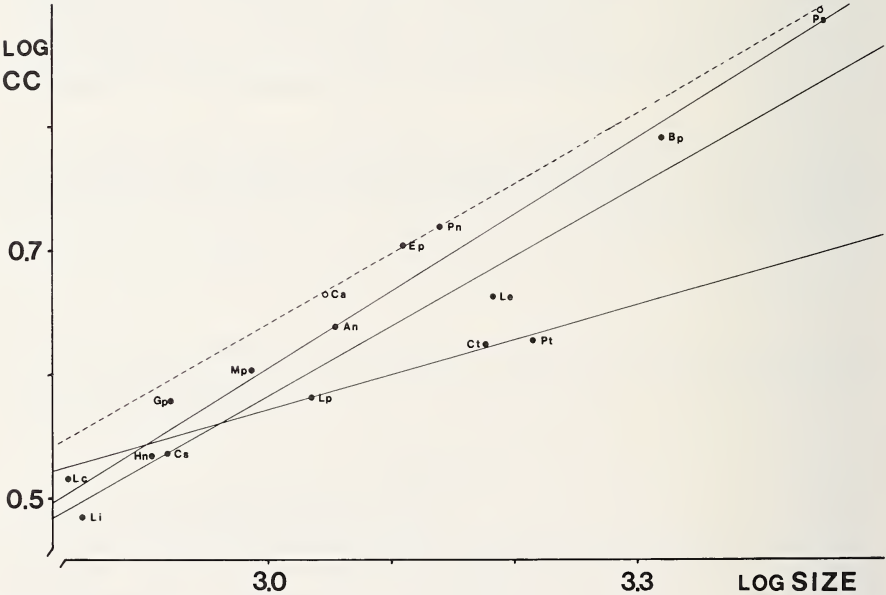


Fig.50: Allometric width over canini to SIZE

Table 12: Allometric proportions: upper tooth row to SIZE

| | MW SIZE | MW OZR | $\tan \alpha$ | r | Lot |
|-----------------------|---------|--------|---------------|--------|---------|
| <i>Carollia</i> | 3.0448 | 0.8689 | 0.6390 | 0.7406 | 0.0021 |
| <i>Phyllostomus</i> | 3.4483 | 1.0673 | 0.2822 | 0.9507 | -0.0066 |
| <i>Brachyphylla</i> | 3.3195 | 0.9923 | 0.5977 | 0.7862 | 0.0078 |
| <i>Erophylla</i> | 3.1089 | 0.8971 | | | 0.0040 |
| <i>Phyllonycteris</i> | 3.1474 | 0.8846 | | | 0.0346 |
| <i>Lionycteris</i> | 2.8499 | 0.7997 | 0.6090 | 0.5469 | -0.0203 |
| <i>Lonchophylla</i> | 3.0317 | 0.9321 | 0.7183 | 0.9708 | -0.0673 |
| <i>Platalina</i> | 3.2137 | 1.0401 | | | -0.0897 |
| <i>Glossophaga</i> | 2.9199 | 0.8711 | 0.6522 | 0.6390 | -0.0588 |
| <i>Monophyllus</i> | 2.9833 | 0.9188 | | | -0.0767 |
| <i>Lichonycteris</i> | 2.8420 | 0.7682 | | | 0.0075 |
| <i>Leptonycteris</i> | 3.1805 | 0.9579 | 0.7942 | 0.6015 | -0.0231 |
| <i>Anoura</i> | 3.0543 | 0.9434 | 0.6900 | 0.6673 | -0.0679 |
| <i>Choeroniscus</i> | 2.9186 | 0.8842 | 0.5966 | 0.7884 | -0.0725 |
| <i>Hylonycteris</i> | 2.9041 | 0.8798 | | | -0.0749 |
| <i>Choeronycteris</i> | 3.1753 | 1.0630 | 1.3399 | 0.8281 | -0.1307 |
| <i>Musonycteris</i> | 3.2070 | 1.4076 | | | -0.4603 |
| Outgroup | 3.1535 | 0.9221 | 0.4701 | 0.6149 | 0.0000 |

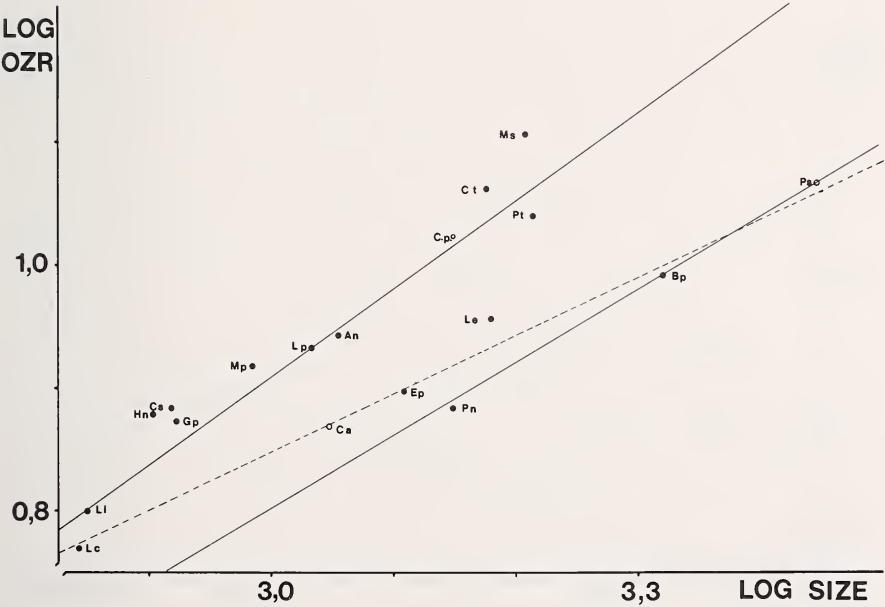


Fig.51: Allometric proportions upper tooth row to SIZE

Table 13: Allometric proportions: length of palate to SIZE

| | MW SIZE | MW GL | $\tan \alpha$ | r | Lot |
|-----------------------|---------|--------|---------------|--------|---------|
| <i>Carollia</i> | 3.0448 | 1.0152 | 0.5367 | 0.8612 | 0.0004 |
| <i>Phyllostomus</i> | 3.4483 | 1.1725 | 0.3515 | 0.9417 | 0.0061 |
| <i>Brachyphylla</i> | 3.3195 | 1.0971 | | | 0.0294 |
| <i>Erophylla</i> | 3.1089 | 1.0385 | | | 0.0030 |
| <i>Phyllonycteris</i> | 3.1474 | 1.0351 | 0.4277 | 0.8212 | 0.0179 |
| <i>Lionycteris</i> | 2.8508 | 0.9834 | | | -0.0462 |
| <i>Lonchophylla</i> | 3.0317 | 1.1499 | 0.5489 | 0.9453 | -0.1396 |
| <i>Platalina</i> | 3.2137 | 1.2813 | | | -0.1975 |
| <i>Glossophaga</i> | 2.9211 | 1.0724 | 0.7368 | 0.6807 | -0.1068 |
| <i>Monophyllus</i> | 2.9833 | 1.0726 | 0.4512 | 0.1410 | -0.0819 |
| <i>Lichonycteris</i> | 2.8414 | 1.0033 | | | -0.0699 |
| <i>Leptonycteris</i> | 3.1805 | 1.1882 | 0.9549 | 0.7639 | -0.1178 |
| <i>Anoura</i> | 3.0543 | 1.1133 | 0.6515 | 0.6451 | -0.0939 |
| <i>Choeroniscus</i> | 2.9186 | 1.1415 | 0.6781 | 0.9537 | -0.1769 |
| <i>Hylonycteris</i> | 2.9045 | 1.1358 | | | -0.1769 |
| <i>Choeronycteris</i> | 3.1753 | 1.2777 | 1.6174 | 0.5810 | -0.2094 |
| <i>Musonycteris</i> | 3.2070 | 1.3554 | | | -0.2743 |
| Outgroup | 3.1565 | 1.0607 | 0.4039 | 0.9802 | 0.0000 |

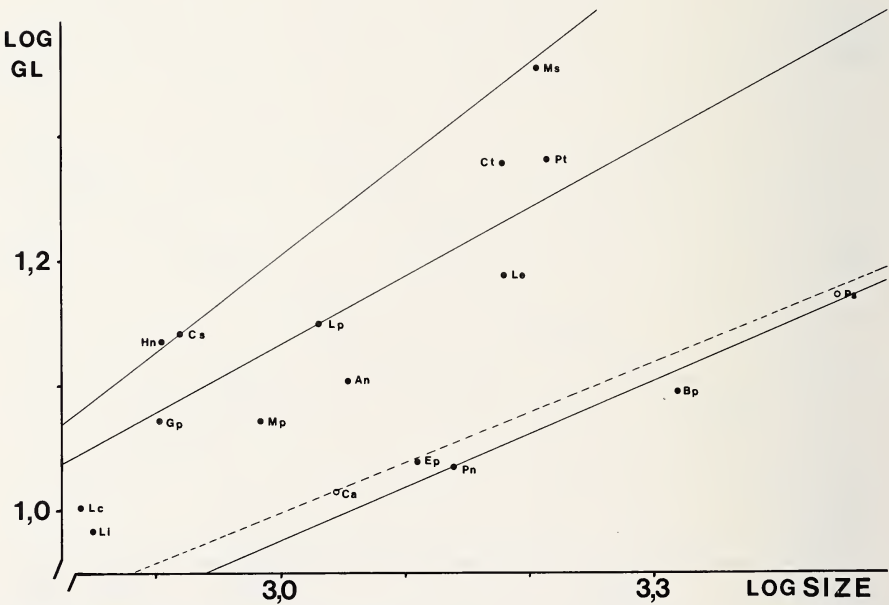


Fig.52: Allometric length of palate to SIZE

Table 14: Allometric proportions: mandible length to SIZE

| | MW SIZE | MW UKL | $\tan \alpha$ | r | Lot |
|-----------------------|---------|--------|---------------|--------|---------|
| <i>Carollia</i> | 3.0448 | 1.1392 | 0.9468 | 0.9939 | 0.0043 |
| <i>Phyllostomus</i> | 3.4483 | 1.3360 | 0.3388 | 0.9833 | -0.0062 |
| <i>Brachyphylla</i> | 3.3195 | 1.2755 | 0.5744 | 0.9456 | -0.0052 |
| <i>Erophylla</i> | 3.0197 | 1.1958 | | | -0.0638 |
| <i>Phyllonycteris</i> | 3.1474 | 1.1922 | 0.2800 | 0.7937 | -0.0013 |
| <i>Lionycteris</i> | 2.8499 | 1.0972 | 0.6295 | 0.7994 | -0.0436 |
| <i>Lonchophylla</i> | 3.0317 | 1.2210 | 0.5743 | 0.9543 | -0.0835 |
| <i>Platalina</i> | 3.2137 | 1.3555 | | | -0.1340 |
| <i>Glossophaga</i> | 2.9199 | 1.1715 | 0.6753 | 0.7311 | -0.0856 |
| <i>Monophyllus</i> | 2.9833 | 1.1702 | | | -0.0550 |
| <i>Lichonycteris</i> | 2.8420 | 1.0961 | | | -0.0462 |
| <i>Leptonycteris</i> | 3.1805 | 1.2660 | 0.3848 | 0.5247 | -0.0598 |
| <i>Anoura</i> | 3.0543 | 1.2244 | 0.4959 | 0.8573 | -0.0765 |
| <i>Choeroniscus</i> | 2.9186 | 1.1863 | 0.6004 | 0.8904 | -0.1010 |
| <i>Hylonycteris</i> | 2.9045 | 1.1691 | | | -0.0903 |
| <i>Choeronycteris</i> | 3.1753 | 1.3297 | 1.3399 | 0.6252 | -0.1259 |
| <i>Musonycteris</i> | 3.2070 | 1.4076 | | | -0.1892 |
| Outgroup | 3.1535 | 1.1937 | 0.4615 | 0.9709 | 0.0000 |

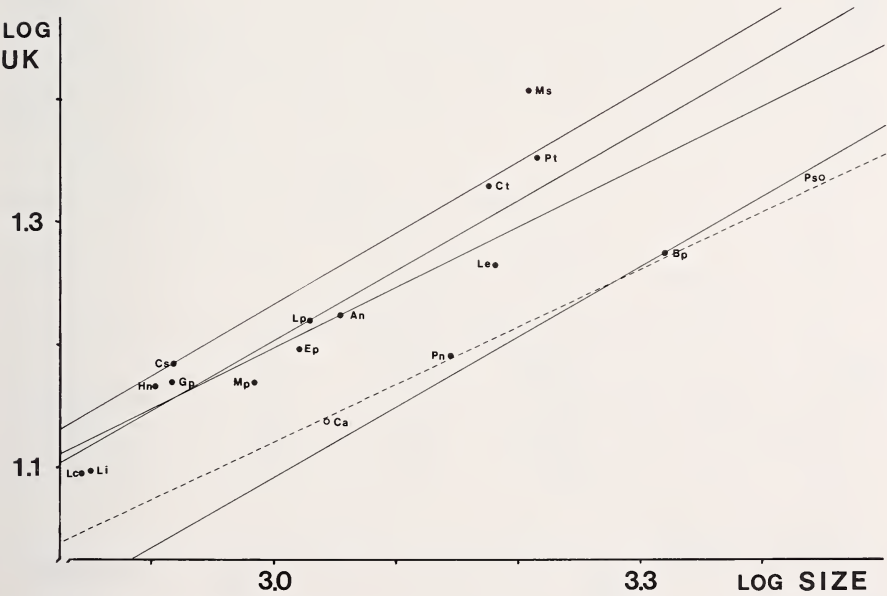


Fig.53: Allometric proportions: mandible length to SIZE

Table 15: Allometric proportions: coronoid height to SIZE

| | MW SIZE | MW CH | $\tan \alpha$ | r | Lot |
|-----------------------|---------|--------|---------------|--------|---------|
| <i>Carollia</i> | 3.0448 | 0.6952 | 0.8863 | 0.8531 | 0.0097 |
| <i>Phyllostomus</i> | 3.4483 | 0.9285 | 0.5110 | 0.9511 | 0.0013 |
| <i>Brachyphylla</i> | 3.3195 | 0.8720 | | | -0.0147 |
| <i>Erophylla</i> | 3.1089 | 0.6486 | | | 0.0920 |
| <i>Phyllonycteris</i> | 3.1374 | 0.6644 | 0.6849 | 0.8619 | 0.0921 |
| <i>Lionycteris</i> | 2.8499 | 0.5633 | | | 0.0330 |
| <i>Lonchophylla</i> | 3.0317 | 0.6494 | 0.5759 | 0.8884 | 0.0482 |
| <i>Platalina</i> | 3.2137 | 0.7539 | | | 0.0451 |
| <i>Glossophaga</i> | 2.9211 | 0.5792 | 0.9510 | 0.7761 | 0.0567 |
| <i>Monophyllus</i> | 2.9833 | 0.5819 | 0.6947 | 0.8010 | 0.0887 |
| <i>Lichonycteris</i> | 2.8387 | 0.5407 | 1.8048 | 0.7686 | 0.0493 |
| <i>Leptonycteris</i> | 3.1805 | 0.6536 | 2.1479 | 0.5752 | 0.1269 |
| <i>Anoura</i> | 3.0543 | 0.6076 | 1.0144 | 0.8302 | 0.1026 |
| <i>Choeroniscus</i> | 2.9186 | 0.4568 | 0.6528 | 0.9366 | 0.1777 |
| <i>Hylonycteris</i> | 2.9045 | 0.5398 | 1.1644 | 0.9821 | 0.0869 |
| <i>Choeronycteris</i> | 3.1753 | 0.6129 | | | 0.1647 |
| <i>Musonycteris</i> | 3.2070 | 0.6267 | | | 0.1686 |
| Outgroup | 3.1808 | 0.7807 | 0.5574 | 0.6799 | 0.0000 |

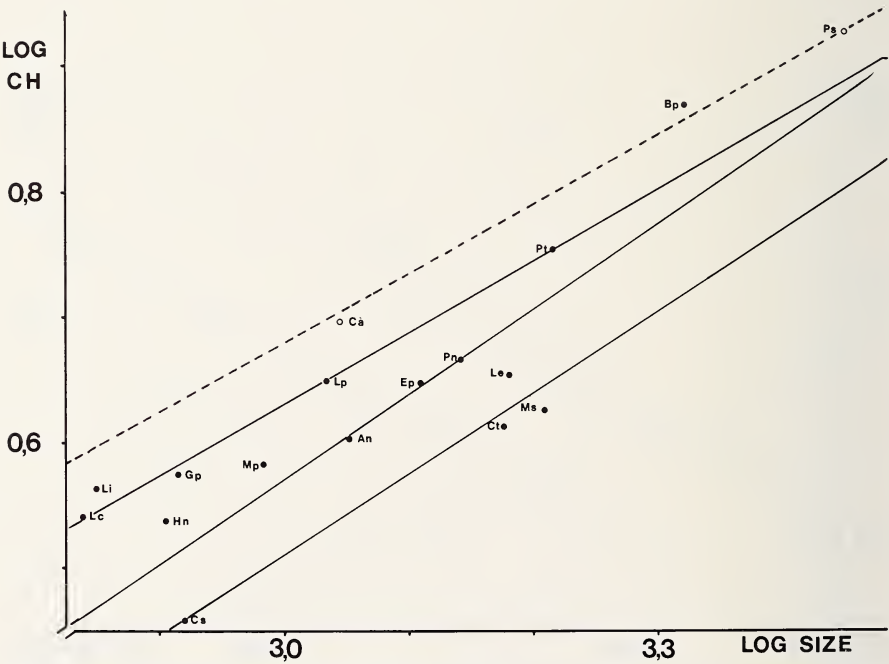


Fig.54: Allometric proportions: coronoid height to SIZE

Table 16: Distances to outgroup

| | GL | OZR | UKL | CH | CC |
|-----------------------|---------|---------|---------|---------|--------|
| <i>Carollia</i> | 0.0004 | 0.0021 | 0.0043 | 0.0097 | 0.0043 |
| <i>Phyllostomus</i> | 0.0061 | -0.0066 | -0.0062 | 0.0013 | 0.0016 |
| <i>Brachyphylla</i> | 0.0294 | 0.0078 | -0.0052 | -0.0147 | 0.0306 |
| <i>Erophylla</i> | 0.0030 | 0.0040 | -0.0638 | 0.0920 | 0.0003 |
| <i>Phyllonycteris</i> | 0.0179 | 0.0346 | -0.0013 | 0.0921 | 0.0010 |
| <i>Lionycteris</i> | -0.0462 | -0.0203 | -0.0436 | 0.0330 | 0.0688 |
| <i>Lonchophylla</i> | -0.1396 | -0.0673 | -0.0835 | 0.0482 | 0.0797 |
| <i>Platalina</i> | -0.1975 | -0.0897 | -0.1340 | 0.0451 | 0.1359 |
| <i>Glossophaga</i> | -0.1068 | -0.0588 | -0.0856 | 0.0567 | 0.0193 |
| <i>Monophyllus</i> | -0.0819 | -0.0767 | -0.0550 | 0.0887 | 0.0282 |
| <i>Lichonycteris</i> | -0.0699 | 0.0075 | -0.0462 | 0.0493 | 0.0354 |
| <i>Leptonycteris</i> | -0.1178 | -0.0231 | -0.0598 | 0.1269 | 0.0827 |
| <i>Anoura</i> | -0.0939 | -0.0679 | -0.0765 | 0.1026 | 0.0341 |
| <i>Choeroniscus</i> | -0.1769 | -0.0725 | -0.1010 | 0.1777 | 0.0600 |
| <i>Hylonycteris</i> | -0.1769 | -0.0749 | -0.0903 | 0.0869 | 0.0536 |
| <i>Choeronycteris</i> | -0.2094 | -0.1307 | -0.1259 | 0.1647 | 0.1173 |
| <i>Musonycteris</i> | -0.2743 | -0.4603 | -0.1892 | 0.1686 | 0.7607 |

Sex dimorphism

Furthermore, it is of interest whether and how sexes differ in these criteria. In this study, this aspect could only be realized to some extent in very common species, as there were only few sufficiently comprehensive samples comprising both sexes. Thus, this aspect is presented only as an example comparing the genera *Anoura*, *Glossophaga* and *Lonchophylla*: tab.17.

Table 17: Allometric proportions: upper tooth row to SIZE (♂-♀)

| Genus | sex | tan α | log b | r | test on difference |
|---------------------|-----|--------------|-------|--------|--------------------|
| <i>Anoura</i> | ♂ | 0.61 | -0.69 | 0.8770 | n.s |
| | ♀ | 0.76 | -0.14 | 0.4619 | |
| <i>Glossophaga</i> | ♂ | 0.67 | -0.36 | 0.6251 | n.s. |
| | ♀ | 0.60 | -0.35 | 0.6932 | |
| <i>Lonchophylla</i> | ♂ | 0.726 | -1.18 | 0.9626 | n.s. |
| | ♀ | 0.756 | -1.34 | 0.9845 | |

DISCUSSION

Morphological adaptations to nectarivory

The Glossophaginae represent small to medium-sized phyllostomid bats with a reduced dentition, distinctly prolonged rostrum and an extremely protrusible tongue - all this indicates adaptations to a diet on nectar and fruit. In ecological terms, these bats may be regarded as nocturnal equivalents of hummingbirds; their evolution having been influenced by several parallel selective forces. There are numerous convergences, such as limits of body weight, hovering ability, elongate tongue, prolongation of the rostral components of the skull.

Gross morphology of the head

Since body shape as a whole hardly varies within the Chiroptera - presumably due to strict requirements on undiminished flight ability (conspicuous differences merely refer to body size, wing area profile, development of the uropatagium and tail length) - their head shape and thus their skull morphology did develop a remarkable morphological variety within the mammals.

As already explained in chapter 1, this considerable variety is, above all, an expression of successful utilization of various food sources with a variety of forms presumably unique on the level of a mammalian order: starting from insectivory, the superfamily Phyllostomatoidea developed any conceivable specialized feeders compatible with flight behaviour: carnivory (Phyllostominae), sanguivory (Desmodontinae), piscivory (Noctilionidae), frugivory (Stenoderminae, Carolliinae, Phyllostominae) and nectarivory (Carolliinae, Phyllostominae, Brachyphyllinae, Phyllonycterinae, Glossophaginae and Lonchophyllinae). Merely browsers and grazers do not exist as an equivalent specialization would have certainly required a digestive system incompatible with flight.

Accordingly, above all, nectarivory is marked by morphological adaptations of the head:

- Prolongation of the muzzle with size diminution of the nose leaf.
- Prolongation and specialization of the tongue (bristle-like papillae, lateral or median nectar groove, musculature of the tongue base) for optimal nectar intake.
- Lower lip with median notch guiding the tongue (lower incisivi very small or missing, the resulting gap allows nectar intake with the tongue with closed jaws).
- Pinnae and tragus are also reduced in size, the ears are rounded, equally broad as long and, compared to other Phyllostomids using echolocation, quite short.

Skull morphology

In osteological terms, this morphological variety of head shape is expressed in a bounty of different skull shapes within the family of the leaf nosed bats (Phyllostomatidae). Especially the visceral skull is an important substrate for evolutionary changes in order to optimize utilization of various food sources. In this respect, the highly specialized flower bats take an extreme position. Besides the prolongation of the viscerocranium and variation of the dentition (referring to form, number and arrangement of the individual tooth types), the adaptations comprise the masticatory and pharynx musculature as well as corresponding bony components of the jaws, their attachment at the braincase and at the mandible.

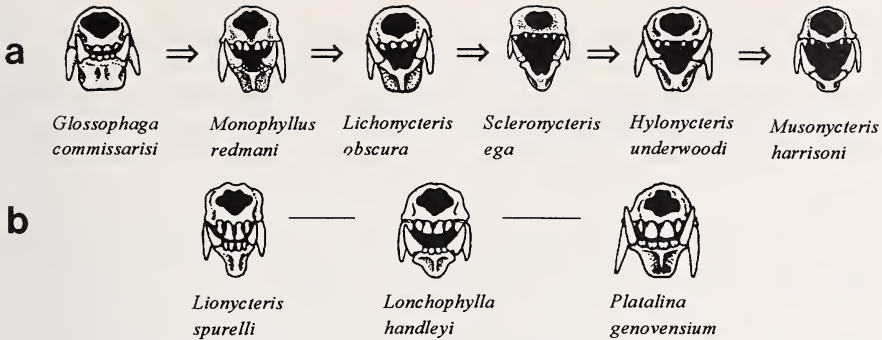


Fig.55: Incisivi within Glossophaginae (a) and Lonchophyllinae (b)

Dentition

Incisivi (fig.55)

The incisors are rudimentary or in some genera the lower ones are lacking completely ("tongue guiding channel"). Comparatively primitive genera with a short rostrum (*Glossophaga*, *Lionycteris*) still have two pairs of incisors in the upper and lower jaw.

In the Lonchophyllinae, the inner upper incisivi are clearly larger than the outer ones. This corresponds to the configuration which appears to be primitive for the entire group. Both, the Phyllostominae and the Carollinae as outgroups, show this pattern of incisivi in the upper jaw.

Within the Glossophaginae, however, this condition remained merely in two *Glossophaga* species, as all other species and genera developed quite considerable modifications: starting from a very uniform incisor pattern (e.g. *Glossophaga commissarisi*) the tooth pairs move apart. In *Leptonycteris* there is just a little median gap between the big but flat inner incisors; *Lichonycteris* developed several gaps distributed evenly between the differently formed upper incisors (the inner ones are flat, the outer ones pointed). This situation with the inner upper incisivi becoming distinctly smaller (*Anoura*) and additionally flattened (*Choeroniscus*, *Hylonycteris*, *Scleronycteris*, *Choeronycteris*) is found in other genera, too. In this evolutionary trend the space for the tongue between the canine teeth also in the upper jaw increases.

Lonchophyllinae, Brachyphyllinae and Phyllonycterinae have two pairs of incisors equal in size in their lower jaw. Though this plesiomorph condition is preserved in *Glossophaga*, in *Monophyllus*, a closely related genus, the lower incisors have become very small and moved apart, both pairs separated by a wide median gap. In *Leptonycteris* there is also a gap between the inner lower incisors, but the inner ones are clearly larger than the outer ones. In *Lichonycteris*, *Anoura*, *Scleronycteris*, *Hylonycteris*, *Choeroniscus* and *Choeronycteris*, the lower incisivi are completely absent, and the lower canine teeth are separated from each other by a deep V-shaped groove above the mandibular symphysis (tongue guiding channel).

Canini

Canines are distinctly developed in all genera, though they remain slim and delicate in the highly specialized nectar feeders. Thus, although the canine teeth seem quite useless for nectar intake, they must have some biological value. Their function, however, is not necessarily corresponding to foraging rather for other biological purposes like grooming

or possibly just stabilizing the closed jaws against distortion when the canines interlock. Freeman (1995) states a considerable tooth-on-tooth wear (thegosis) on the anterior surface of upper canines in nectarivorous microchiropterans. This is interpreted as indicator for tight embracement of lower canines by the upper ones to support the jaw during the rapid movement of the tongue during feeding.

Premolars

Within the Lonchophyllinae, *Lionycteris* still bears very strong premolars resembling canine teeth. In *Brachyphylla*, the posterior upper premolars also are of similar relative size to the canine tooth, the anterior one, however, remaining very small as specific for this genus. In the course of further specialization the premolars become tricuspid, moving apart widely as the jaw bone prolongates. Only in *Anoura* - unique among phyllostomids - there are three premolars on each side of the upper jaw. This situation represents a virtually reverse evolutionary trend and possibly originated from a secondary doubling of the anterior premolars (Phillips cited by Koopman, pers. comm. 1991). This secondary replenishment of the gap between the upper canine tooth and the upper P³ having developed in the course of rostrum prolongation may derive its ecological significance from the high percentage of insect food which has been reported for this genus.

Molar teeth

Considerable changes occurred in the molar teeth: whereas *Glossophaga* and *Lionycteris* still show the dilambdodont profile of the masticatory surface typical of insectivorous bats, *Choeroniscus*, *Hylonycteris* and *Choeronycteris* hardly have any crown cusps nor W-shaped ectolophis.

With increasing jaw length, the molar teeth increasingly moved apart, too. Thus, in the very long-muzzled forms there is apparently no masticatory function any more. Furthermore, the crowns are not only narrow in top view, but also hardly project beyond the gums. The masticatory surfaces are largely reduced; leaving only few pointed cusps (premolariform) with a physiological value on which we only can speculate. They appear of very little use in food preparation and do not seem to be essential for a nectarivorous way of life.

Rostrum

Within the Phyllostomatidae, the specialized nectar feeding bats of the New World are characterized by a prolongation of the visceral cranium involving the maxillaria, nasalia, palatina, the vomer and the mandibulae.

The degree of this prolongation varies considerably between single species and may thus be considered an evidence of the degree of feeding specialization. Species preferring varied diet like *Glossophaga* or *Lionycteris* have shorter rostra than highly specialized nectar feeders like *Choeronycteris*.

Within a genus these proportions are also influenced by body size of the species. Smaller species showing comparatively larger braincases and shorter jaw lengths, respectively. In this case, the construction principles are just the same despite their differing proportions. Differences in proportion are found in closely related taxa (subspecies, species) whereas different construction principles occur beyond the species level.

In contrast to the short viscerocranium of the predominantly frugivorous genus *Brachyphylla*, the Phyllonycterinae (*Erophylla* and *Phyllonycteris*) were subject to a moderate muzzle prolongation as they specialized in nectarivory. The situation is the same

for *Lionycteris* within the Lonchophyllinae and for *Glossophaga* within the Glossophaginae.

Within the genus *Lonchophylla* there are already some species with relative long rostra; *L. thomasi* has a comparatively short rostrum; this feature, however, depending on body size: within each genus, relative rostrum length increases allometrically with body size. The longest rostrum of all Lonchophyllinae is found in the genus *Platalina* with the palate length comprising more than half of the total skull length.

Also within the Glossophaginae, the smaller species show relatively short rostra (*Lichonycteris obscura*, *Choeroniscus godmani*). There are, however, considerable differences between genera of equal size (*Leptonycteris* and *Choeronycteris*). As an extreme, the Mexican banana bat *Choeronycteris harrisoni* has the longest rostrum (in relative and absolute terms) among all nectar feeding bats.

Forehead

Since rostrum length is emphasized, the development of the forehead is increasingly restricted: interorbital and postorbital width are relatively small and, in the extreme case, no longer distinguishable from each other any more. Similar to other extremely long-jawed mammals (cf. *Myrmecophaga*) the Glossophaginae lack a demarcation from the orbitae by visible orbital processes.

Zygomatic arches

Reduction of the zygomatic arches corresponds to the significance of the masticatory musculature which is reduced with increasing specialization. These structures are often damaged during preparation or inadvertently totally removed (in Husson 1965, the missing zygomatic arches were erroneously recorded as a determination feature within the Glossophaginae sensu strictu). Whereas neither the Carolliinae nor the Lonchophyllinae

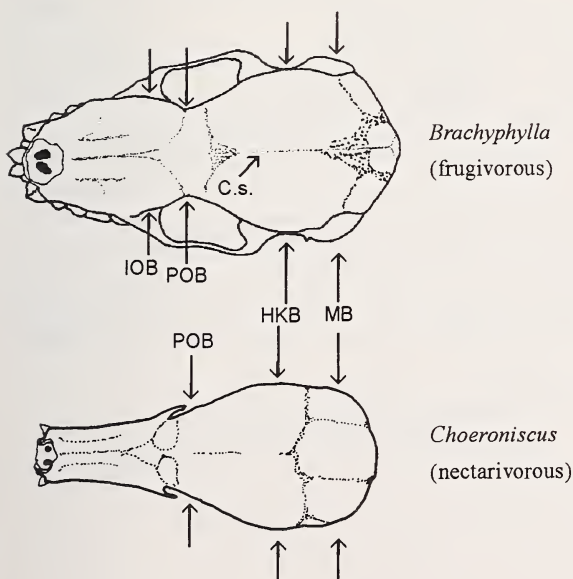


Fig.56: Skulls of bats with different diet.

IOB = interorbital width
POB = postorbital width
HKB = width of braincase
MB = mastoid width
C.s. = crista sagittalis

have any bony zygomatic arches, these structures remain detectable at least by X-ray prior to preparation (*Choeroniscus*). Only in the extremely long-nosed species of the genus *Choeronycteris* no zygomatic arches could be found.

Braincase (fig.56)

Although cranial modifications with reference to nectarivory predominantly manifest themselves in the viscerocranium, in some respects also the braincase of nectar feeding bats is clearly distinguishable from that of other phyllostomids. This is principally due to receding significance of the masticatory muscles; as the origin of the M. temporalis does not express itself at the vertex of the bone surface any more.

In the predominantly frugivorous genus *Brachyphylla*, a Crista sagittalis is just present to some extent. In all genera of the remaining nectarivorous subfamilies this characteristic lacks in both sexes.

The Pars petrosa is merely developed (i.e. = in specialized nectar feeders like *Choeroniscus*, the width of the braincase exceeds mastoid width).

Skull base (fig.57)

In most species, the base of the neurocranium and the palate are arranged in an almost parallel way, i.e. there are no angles between both areas. On the other hand, the outgroup genera of Phyllostominae and Carolliinae, but also Brachyphyllinae and Phyllonycterinae show an inclination of the palate plane towards the skull base. In *Choeroniscus* and *Hylonycteris*, there is a striking elevation of the brain capsule against the palate plane (fig.57). This affects measurements of skull height in so far as the slide caliper rests on the hamuli rather than the Bullae tympanicae. Whether this arrangement is possibly significant for some special form of nectarivory cannot be assessed at the moment. In terms of functional morphology, there is a reference to the position of the mandibular joint. In comparison, the even longer skull of *Choeronycteris* tends to the opposite angular inclination. This might be due to mechanical constraints which require the elongate rostrum bent down in ventral direction to gain stability.

The convexities of the basisphenoid vary considerably between the species of a genus, too the "basisphenoid pits" represent an essential determination feature within the genus *Glossophaga* (Webster & Jones 1980).

One of the strangest features within the family is the extreme prolongation of the pterygoid processes (hamuli). In *Choeroniscus* and *Choeronycteris* they are extending to the Bullae tympanicae with lateral widenings. Functional significance may not have been interpreted properly on the basis of the preserved material. The soft palate is, however, probably prolonged in occipital direction: the hamuli function as an abutment (roller bearing) against the tendons of the M. levator velum palatini. Functionally, this might improve efficiency of the swallowing motor apparatus during high-frequency tongue movements.

Phyllonycteris



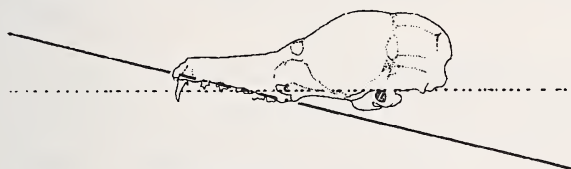
clinorhynchic

Monophyllus



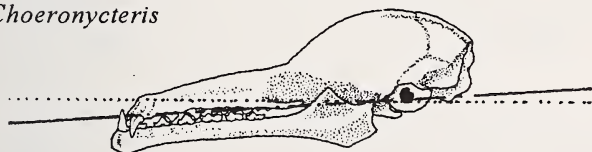
orthocranic

Choeroniscus



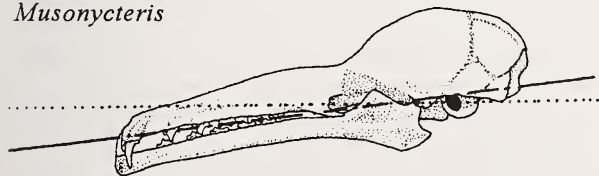
aiorrhynchic

Choeronycteris



clinorhynchic

Musonycteris



clinorhynchic

Fig.57: Orientation of the skull base in Phyllonycterinae and Glossophaginae

Mandible (fig.58)

Whereas *Carollia* and *Phyllostomus*, but also *Brachyphylla* have strong mandibles, increasing specialization brings about a flattening of the Ramus mandibularis, the Processus coronoideus becomes relatively smaller with increasing length of the mandible. The highly specialized nectar bats show a characteristic ridge (symphysal ridge) at the mandibular symphysis, giving the lower jaw a "bulb bow profile" in lateral view - probably due to reduction of the lower incisivi and the development of a V-shaped notching of the mandibular tip and of the median lower lip forming a tongue guiding channel. None of the basic genera shows a comparable feature. It obviously may serve to stabilize the fused mandibular tip as the notching between the lower canini has increased to an extent that afflicts the mandibular suture. According to Freeman (1995) all nectarivorous bats have fused mandibulae, which probably increases stability of the jaws but also could result from less need for minute adjustments at the symphysis in order to precise registration of cheek teeth.

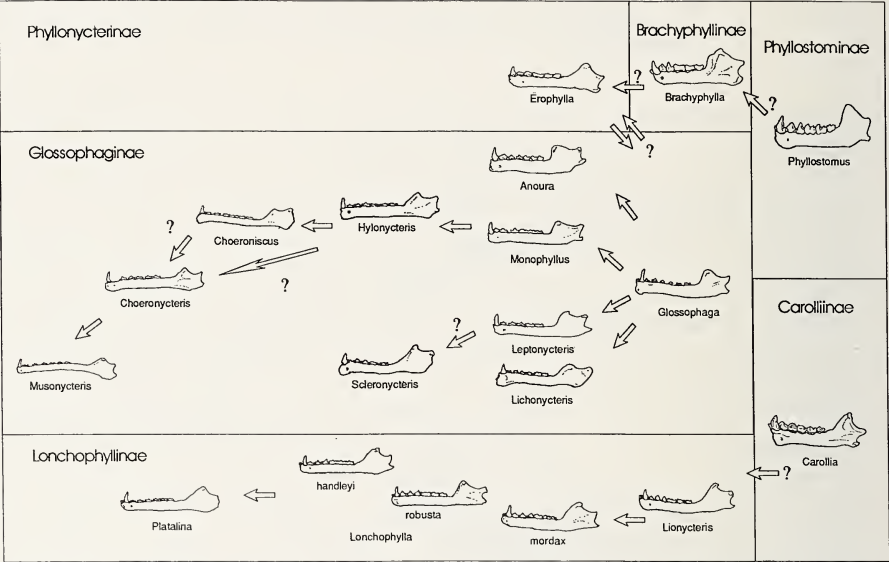


Fig.58: Mandibles of the phyllostomid families examined in lateral view. Specialization on nectar feeding increases from right to left. For clarifying the construction principles, the jaws were drawn in the same size, ignoring the scale. The arrows indicate evolutionary trends of mandible construction as derivations of common features

Craniometry

Univariate Analysis

The results of univariate analysis of the skull measures are given in tab.4a, b (p. 64-66) for all taxa examined. Only for individual species the mean has been worked out.

These data reveal, however, that their range may overlap between individual species of a genus, even if the mean values significantly differ from each other.

Only those taxa comprising sufficient numbers of specimen were processed statistically, the rare species allow nothing than individual records.

Sexual dimorphism:

- Within the genus *Phyllostomus* which was examined as an outgroup, almost all skull measures of male *P. hastatus* - a very large species - range above the female ones. Swanepoel & Genoways (1979) recorded the forearm lengths and seven skull measures of eight individuals collected at different locations showing that the relations between the sexes appeared similar in forearm length. In biological terms, this difference in size may be explained by the social system of these bats; in *Phyllostomus hastatus*, the males establish harem groups within territories (Koeppke 1987).
- In all species of *Choeroniscus* examined so far, the female length values of the skull exceed those of the males in a statistically significant way. Probably, this difference in size allows these bats to utilize their resources in a more efficient way, as they live in very small family groups (Koeppke 1987). Though the rain forest teems with chiropterophilic flowering plant species, they occur in quite low density. Probably it is only due to slightly diverging niches that both sexes may survive sharing the same habitat. Appropriate evidence is, however, still to come. It is quite as probable that body size is determined by social factors rather involving the females.
- The only measured male of *Lonchophylla robusta* is definitely larger than all the female individuals - unlike smaller species of the genus where the females are larger. In *L. handleyi* which grows even a bit larger, the data of the males exceed those of the females in 12 of 17 parameters on the average, but based on the available sample this could not be secured statistically.

Females larger than males are not uncommon among bats. This may be a response to the increased energetic demands of flight in pregnant females (Myers 1978; Williams & Findley 1978). Williams & Findley (1978) however suggested other factors like thermoregulation and fat storage might be more important determinants of body size of females than adaptations to flight (Sahley et al. 1995).

Skull proportions

An account of both, the absolute size relations and adaptive degree of the species examined, gives the summary of measurement relations of the 'Results': this refers to rostrum length and gives evidence of decreasing functional significance of the masticatory apparatus.

1) Proportions of total skull length to length of the palataea: Although palate length is a part of total skull length, it remains a useful measure for recording the size of the visceral skull.

Both phyllonycterine genera (*Phyllonycteris* and *Erophylla*) perform an even higher quotient (= shorter bony palate) in tab. 5 than the outgroup (*Carollia*). Here, there must be considered that both genera have a V-shaped edge of the palate running at a very acute angle and thus affecting the value in this parameter (but not total rostrum length).

Furthermore, this ranking essentially represents the degree of specialization within the nectar feeders: *Lionycteris* and *Glossophaga* / *Monophyllus* proved to be basal forms in this respect, *Choeroniscus* and *Choeronycteris* the most specialized ones.

2) Total skull length to length of upper tooth row: Some aspects in dentition which cannot be explained exclusively by rostrum prolongation prove inconvenient: the number of teeth varies considerably among the genera (cf. dental formulas). In the course of rostrum prolongation only the distance between the postcanine teeth is enlarged in all long-headed species, but the measured length may consist of just four to six teeth.

Thus, within the resulting order of relative lengths of the maxillar tooth row (the smallest value for quotients represents the longest tooth row) the dental formula which differs from the original pattern of the subfamily (five postcanine teeth on one half of the upper jaw) must be taken into consideration: in *Leptoncyteris* and *Lichonycteris* there are two premolars and molars each on one half of the upper jaw, and in *Anoura* there are 6 teeth in total forming the postcanine tooth row. In comparison, there is an extreme long tooth row in *Monophyllus*. Though considered primitive by other characteristics, in this respect, this genus is in no way inferior to the highly specialized species.

3) Height of the braincase to palate length: Whereas total skull length in 1) certainly shows a trend to muzzle prolongation, this will not be expected for height of the braincase. Size and shape of the braincase are determined primarily by brain morphology, and in forms with strong masticatory musculature there is an additional influence by the musculature originating at the braincase (Crista sagittalis). As the latter is weakly developed in all Glossophaginae (revealing a decrease of masticatory function in food intake), it does not influence the height of the braincase at all.

The position of *Phyllostomus* within the order of the quotients remains remarkable, suggesting that the palate is relatively longer compared to braincase height - in this case, the quotient is determined by the Crista sagittalis with an incomparable brain case height.

4) Total skull length to coronoid height: The height of the coronoid process at the Ramus mandibularis refers to masticatory functions of the species examined: here the M. temporalis which is essential for efficient snapping, inserts at the mandible. As specialization on nectarivory increases, this musculature becomes less important. The quotient of total skull length and coronoid height indicates which of the genera experienced the most distinctive prolongation of the visceral skull with a simultaneous reduction of the masticatory function.

5) Height of the braincase to coronoid height: Apart from the relation to total length, the comparison of a quantity independent of rostrum prolongation as braincase height and coronoid height does make sense as a measure reflecting the functional reduction of the jaw apparatus: in this context, the otherwise very long-headed *Platylina* takes a basal rank, and with a quotient of 2.12, *Hylonycteris* shares the same level with the unspecialized genus *Lionycteris* (2.13). In contrast to the comparison SGL to CH, also *Musonycteris* has shifted to a middle position, and *Erophylla* stands out with a quite flat mandible compared to the height of the braincase (2.17). These partly different orders in both quotients are strongly determined by absolute skull size - the denominator - braincase size - is comparatively larger in smaller individuals. This supports once more the necessity of performing allometric comparisons, too.

6) Mandible length to coronoid height: The length of the mandible may be referred to as a reliable measure for the length of the viscerocranium. Setting mandible length to coronoid height also results in a representative perspective for the extent of specialization in the genera examined. The larger the quotient, the longer the mandible related to coronoid height. In addition to its significance, the value of mandible length is reinforced by the negative trend of coronoid height in the course of higher specialization on nectar and pollen feeding.

Allometrics

Intergeneric allometrics

Although allometric approaches usually are chosen in different size relations of the systematic sample taxa (in individuals of equal size, proportion differences would stand out already by simple comparison of the values), it may nevertheless be useful to analyse allometries even in individuals of almost same size, as allometries sometimes do differ in individual features even in species of equal dimensions.

Referring to nectar intake, some specialized flower bats show an extremely prolonged rostrum. Relative length to total skull length varies considerably between individual species. So, there are differences in relative length of the visceral skull both between the species of a genus and between individual genera. Furthermore, the species show considerable differences in body size (factor up to 1.8). Thus, it was to examine whether different proportions can be explained by allometry - and whether the rostra of different size follow the same principles of construction.

From the total of 17 skull measures involved in univariate analysis, five allometric parameters which are especially affected by rostrum prolongation were related to SIZE:

1. Width over canini (CC) (figs. 61-62): This measure gives information on terminal rostrum width and affects the geometry of the visceral skull with respect to its relative size.
2. Upper tooth row (OZR) (figs. 63-65): Distinct assignment of the canine, premolar and molar alveoli to the maxillaria allows to determine relative length of these maxillar bones. It remains, however, important to consider the dental formula and the number of postcanine teeth, respectively, in the upper jaw.
3. Length of the palate (GL) (figs. 66-70): Apart from the maxillaria, primarily the palatinae become stretched in the course of rostrum prolongation. Thus, this measure compared to the braincase (SIZE) also gives information on relative prolongation of the visceral skull. The conspicuous contours of the proximal palate edge vary in individual species between sharply V-shaped over smoothly U-shaped up to a weakly rounded, almost straight form. Thus, this measure is considerably determined by the construction of the bony palate.
4. Length of mandible (UKL) (fig.71): This measure reflects a very useful correlate of the respective rostrum length. Compared to OZR and GL it has the advantage that a) the measure also comprises the rostral part anterior of the canines, b) none of the constructions not originally associated with the visceral skull will affect the measure, and c) the measures are easily accessible.
5. Coronoid height (CH) (fig.72): Representing an expression for the functional significance of the M. temporalis for the interlocking jaws, the relation of coronoid height to braincase (SIZE) gives information on relative importance of the chewing process, thus considering an important aspect of functional morphology in the analysis of rostrum prolongation.

The data given earlier (p.66) lead to the following statements:

Width over canini (C-C): In the genera *Carollia* and *Phyllostomus* summarized in the outgroup, the canine distances are comparatively wider than in the Glossophaginae and Lonchophyllinae (fig.50, tab.5).

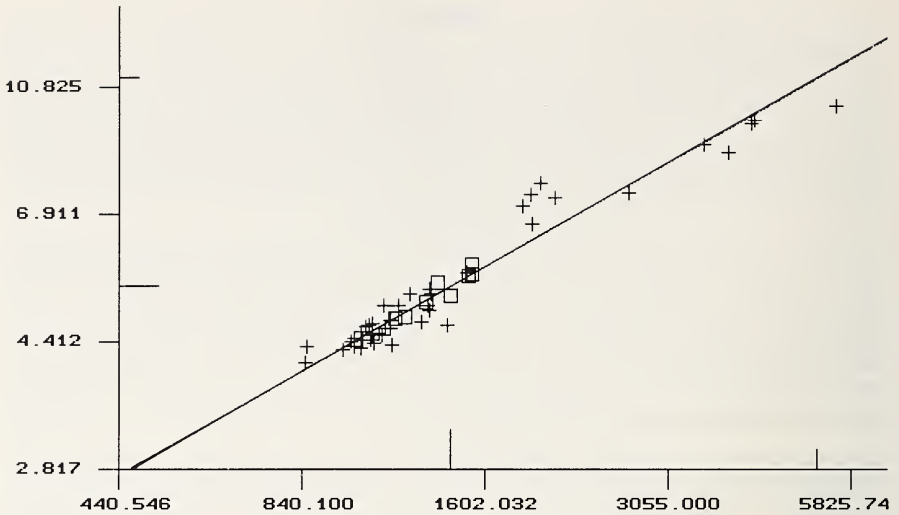


Fig.59: Relation SIZE to width over canini: comparison between *Phyllonycteris* (□) and outgroup (+)

With increasing skull size, the anterior width of the palate increases to a proportionally less extent, the gradient of the reduced elliptic major axis clearly remaining below 45 degrees ($\tan \alpha = 0,57$). It is, however, remarkable that the genera *Erophylla* and *Phyllonycteris* having been summarized within the subfamily Phyllonycterinae do not differ from the outgroup in this respect (fig.59).

In the Glossophaginae, size-dependent shift in proportion follows the same pattern; the distances between the canine teeth are, however, smaller at equal body size in a genus-

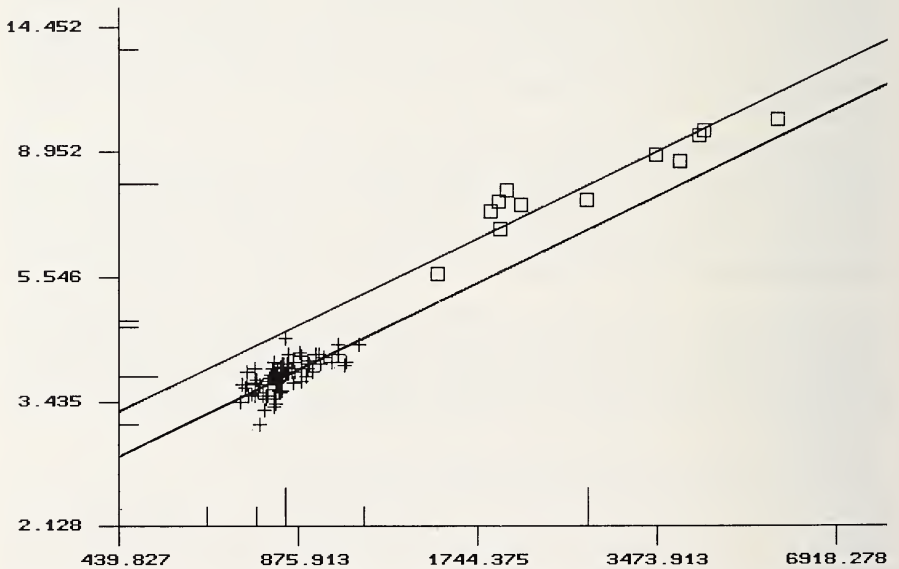


Fig.60: Relation SIZE to width over canini: comparison between *Glossophaga* (□), *Phyllostomus* (+)

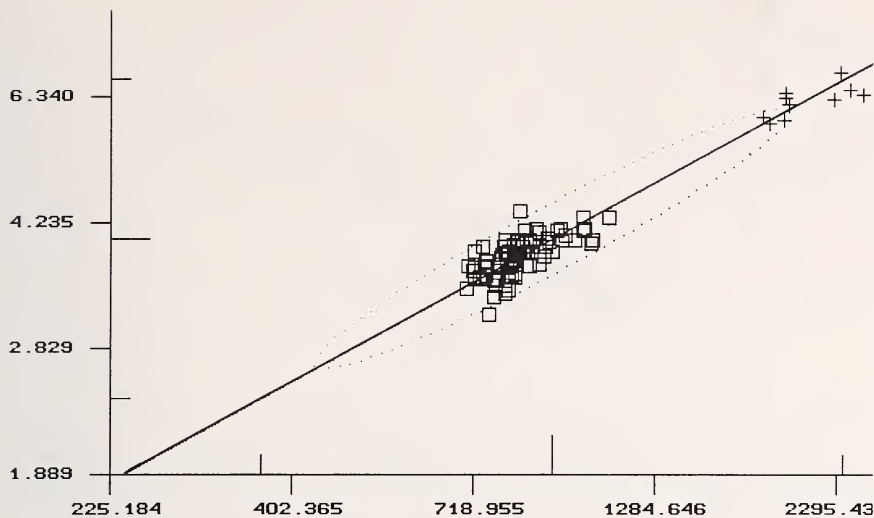


Fig.61: Relation SIZE to width over canini: comparison between *Glossophaga* (□) and *Brachyphylla* (+)

specific way, e.g. the rostra are narrower at their tip than in the outgroup (fig.60). This also applies to *Brachyphylla*, although in many other respects this genus approaches the outgroup much closer than other nectar feeding bats. This is partly due to their considerably differing skull geometry; in basal view, the palate appears rounded in a trapezoid way (the width of the palate over the second molar tooth ist much larger than over the canines, fig.61).

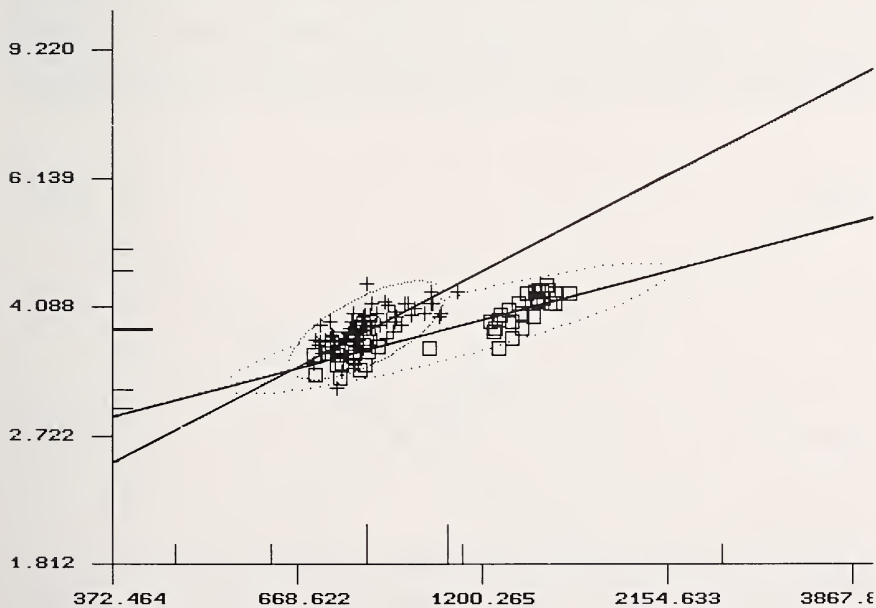


Fig.62: Relation SIZE to width over canini: comparison between *Glossophaga* (□) and *Lonchophylla* (+)

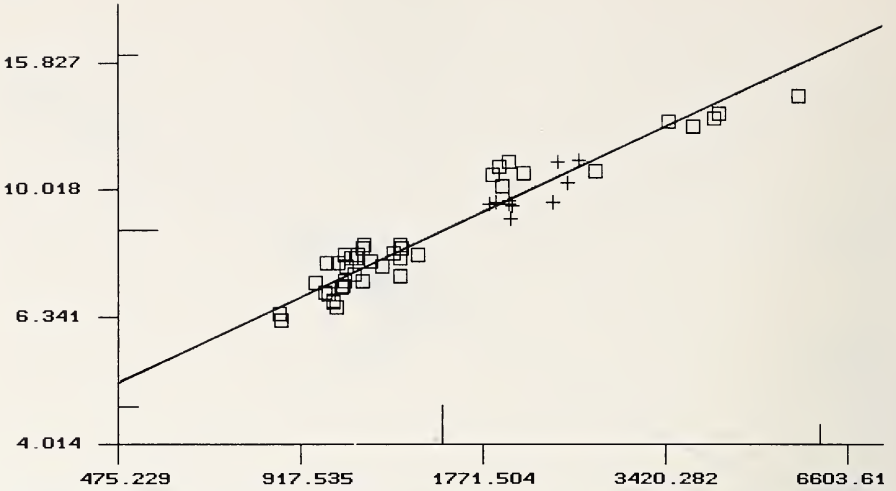


Fig.63: Relation SIZE to upper tooth row: comparison between *Brachyphylla* (+) and outgroup (□)

Still, the lower gradient of the reduced major axis in *Lonchophylla* combined with a high correlation coefficient remains to be interpreted. Also here, an acute-angled geometry of the palate weakens proportional shifts in size alterations (figs.50, 62).

Upper tooth row (OZR): Referring to the length of the postcanine tooth row in the upper jaw, the basic subfamilies Brachyphyllinae and Phyllonycterinae do not differ from the outgroup (cf. figs.51, 63).

In size-dependent comparison of proportions, also the glossophagine genera *Lichonycteris* (fig.51) and *Leptonycteris* (figs.51, 64) closely approach the allometric line characterizing the outgroup - despite a condition of higher specialization in other features, their maxillary tooth row does not exceed that of *Carollia*, *Phyllostomus*, *Brachyphylla*, *Erophylla* and *Phyllonycteris* in length. The reason is quite simple: in both genera, there are only two

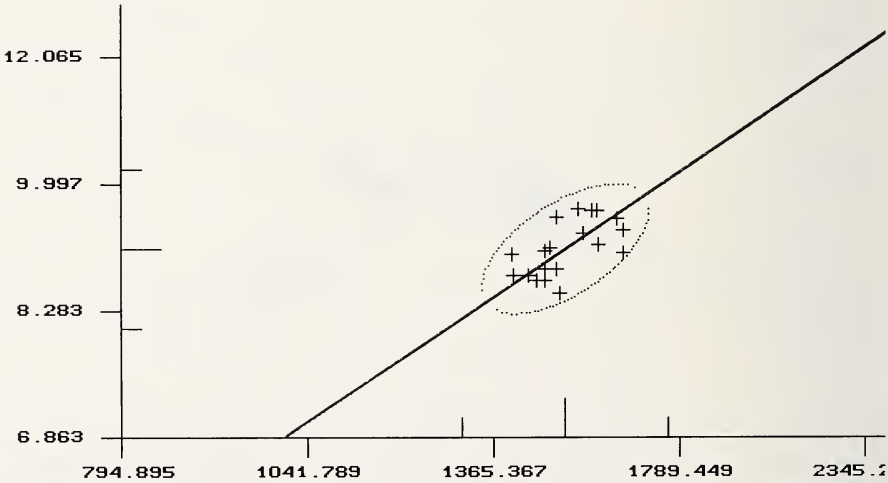


Fig.64: Relation SIZE to upper tooth row for *Leptonycteris*

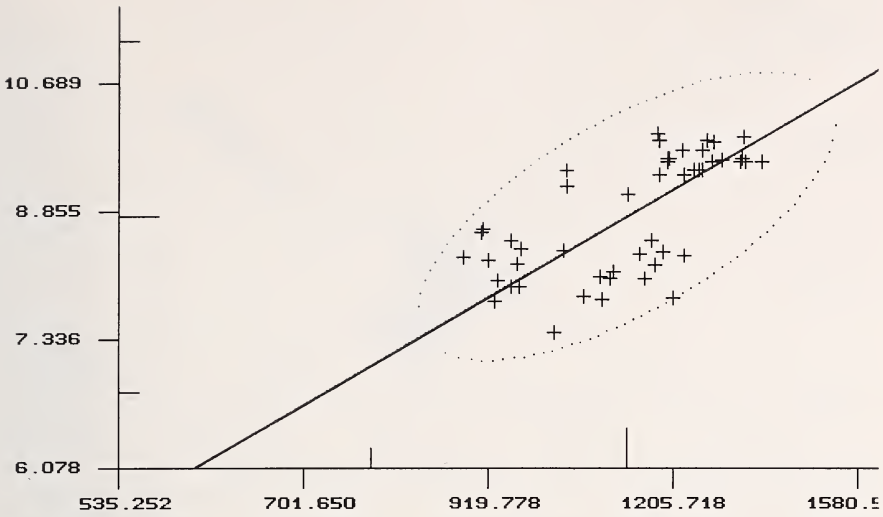


Fig.65: Relation SIZE to upper tooth row for *Anoura*

molars on each half of the upper jaw (figs.63 and 64). With respect to this feature, the remaining Glossophaginae and Lonchophyllinae equipped with five postcanine teeth, are subject to the same allometric conditions. It is, however, remarkable that *Anoura* (figs.51, 65) does not show a larger integration constant although it has more teeth (3 premolars in the upper jaw), as in the other genera, with increasing size the large number is superimposed by larger interdental distances within the length of this measure.

Length of the palate (GL): With respect to statistically securable allometric conditions of this skull measure, *Brachyphylla*, *Erophylla* and *Phyllonycteris* correspond to the outgroup in this parameter, too. Although the random samples of *Brachyphylla* and *Phyllonycteris*

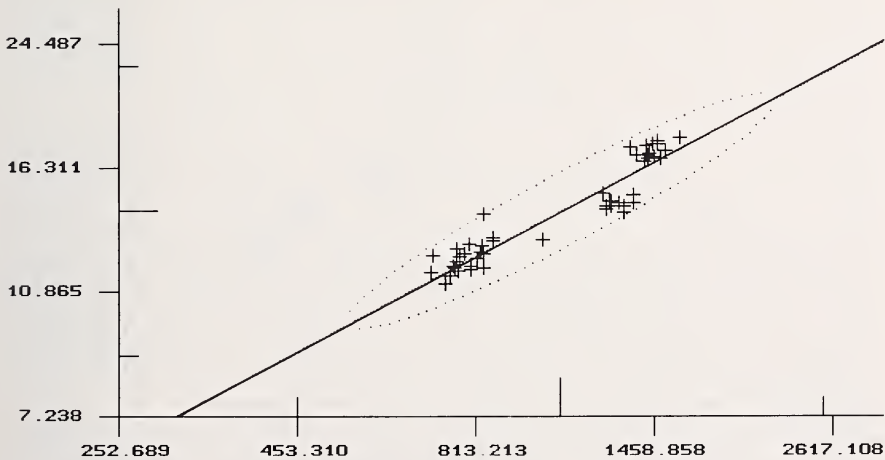


Fig.66: *Lonchophylla*: relation between SIZE and palate length

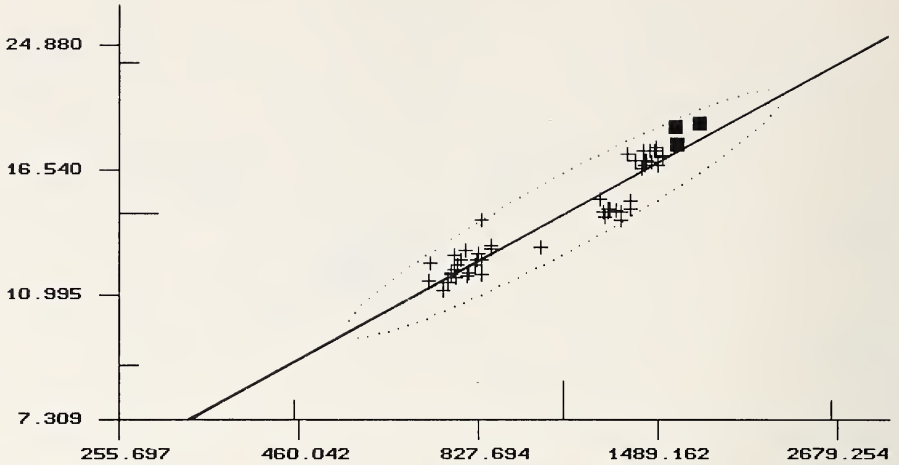


Fig.67: Relation SIZE to palate length: *Lonchophylla* (+) and *Platalina* (■)

differ with $p < 0.05$ from those of the outgroup, the slopes of the reduced major axes of the distribution do not.

The proportional shift of relative palate length remains inconsistent in the Glossophaginae and Lonchophyllinae. There is no doubt that the gradient of the reduced major axes in all genera, where correlation could be secured, is distinctly below 45 degrees and thus not to be secured against the outgroup, but their integration constants do show considerable differences.

Lionycteris, *Lichonycteris*, *Leptonycteris*, *Monophyllus* and *Anoura* have comparatively short palates which nevertheless exceed those of the outgroup in length. The genera to which the respective subfamilies (*Glossophaga* and *Lonchophylla*) owe their name show a slightly higher level (longer palates).

Compared to the outgroup, the palate of *Platalina* is relatively longer (0.1975) than in the smaller *Lonchophylla* (0.1396), but the position of the mean value in the double logarithmic coordinate system closely approaches the reduced elliptic major axis of *Lonchophylla* (fig.66, 67). This means the relatively more elongate palate may be explained by allometry; the principles of construction are, thus, the same.

The extremely elongate palates of *Choeroniscus*, *Hylonycteris* and *Choeronycteris* (*C. mexicana* and *C. (=Musonycteris) harrisoni*) are still to be interpreted: in *Choeroniscus*, there is a transposition of the reduced major axis with respect to the remaining Glossophaginae (figs.52, 68). Here we find a different genus-specific structural feature: even very small *C. godmani* have a much longer palate than a *Lichonycteris* or *Lionycteris* of the same size. Besides the angular elevation of the palatal area in relation to skull base, *Hylonycteris* and *Choeroniscus* share a bony palate which is considerably prolonged in occipital direction. This functional significance of this apparently derived feature cannot immediately be related to nectarivory. I would regard this as systematically useful evidence on close relationship of both genera.

Referring to this structural feature, the position of *Musonycteris* in the double logarithmic coordinate system gives evidence on close relationship to *Choeroniscus*. Interpretation of

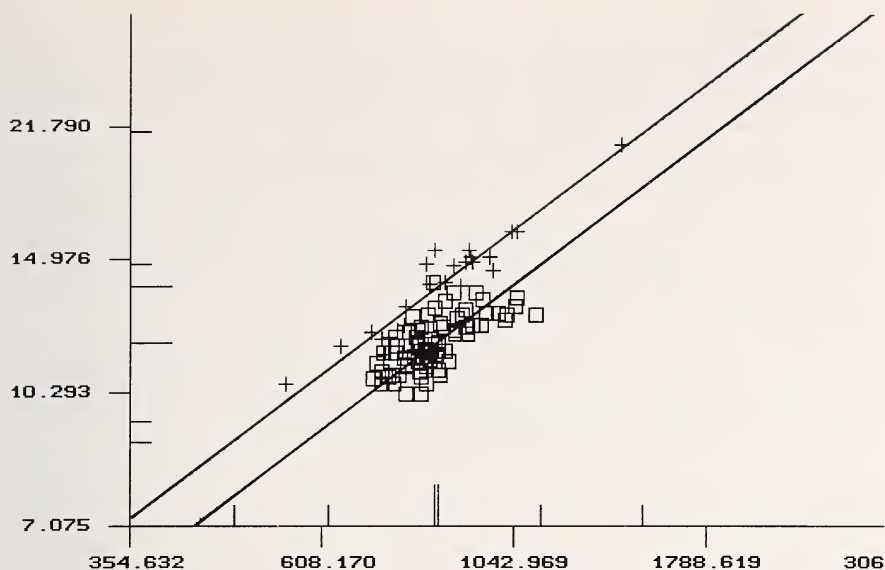


Fig.68: Relation SIZE to palate length: comparison between *Choeroniscus* (+), *Glossophaga* (□)

the allometries is, however, hindered by a relatively shorter palate in *C. mexicana*: here the reduced major axis of *C. mexicana* - though statistically not securable due to the small random samples with a correlation coefficient of 0.5810 - has an extremely steep slope (with a tan a of 1.6174) so with increasing size that the position of *Musonycteris* - despite

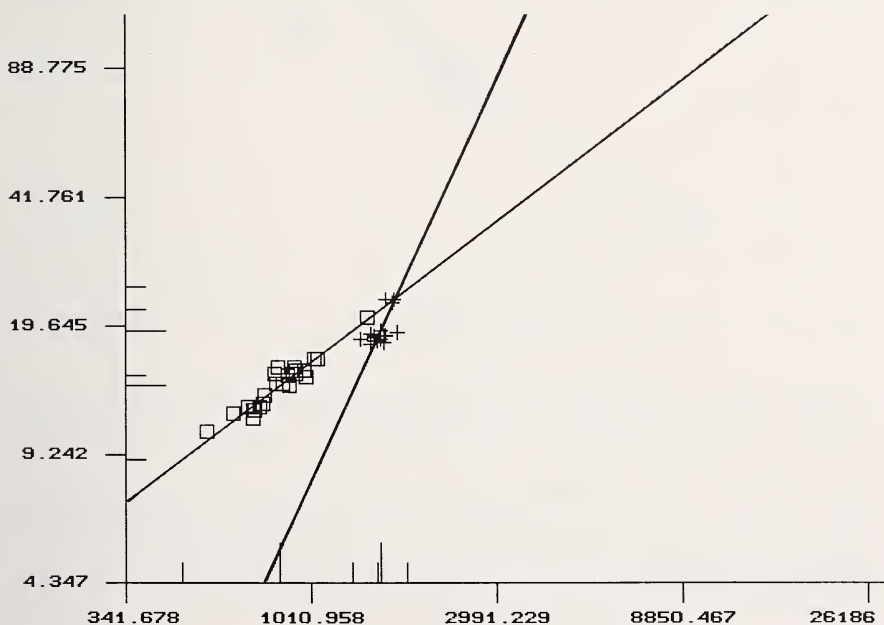


Fig.69: Relation SIZE to palate length: comparison between *Choeroniscus* (□) and *Choeronycteris* (+)

of its different construction - comes up to values which would have been expected for *Choeroniscus*. This manifests itself by intrageneric allometrical calculation of a common random sample comprising *C. mexicana* and *C. harrisoni* (fig.69): they significantly differ from *Choeroniscus* both in the gradient and in the distribution ellipse ($p < 0.05$).

Length of mandible (UKL): Allometric regression of this measure to the reference quantity SIZE results in similar groupings: once more, *Brachyphylla* and *Phyllonycteris* approach the allometric line (reduced major axis) of the outgroup (*Carollia* and *Phyllostomus*). In this parameter, the mean values of *Erophylla* differ from *Phyllonycteris* by a mandible length with proportions resembling those of the remaining basic glossophagines and lonchophyllines.

Furthermore, the integration constants of *Choeroniscus*, *Hylonycteris* and *Choeronycteris* are more distant from the outgroup. In this parameter even *Platalina* matches distances to the outgroup usually applying to extremely long-skulled bats (fig.70, tab.8), subsequently following the allometries calculated for the genus *Lonchophylla*.

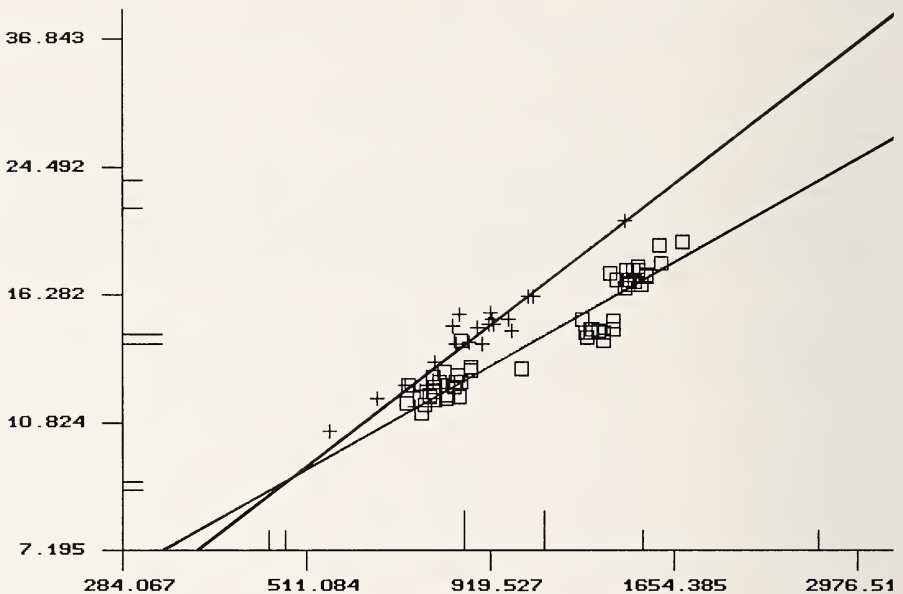


Fig.70: Relation SIZE to mandible length: comparison between *Choeroniscus* (+) and *Lonchophylla* + *Platalina* (□)

Once more, *Musonycteris* sticks out within this comparison. Though it is about the size of *Platalina*, it shows a distinctly more elongate mandible, in this respect even exceeding *Choeronycteris mexicana* by far.

Coronoid height (CH): In the double logarithmic representation of regression of coronoid height to SIZE, the situation is reversed: the Ramus mandibularis is strongest within the outgroup members and in the individuals with the relatively longest rostra, the rami of the mandible are more flattened. Thus, the reduced major axis of the outgroup runs above, and deviations of individual genera are represented by positive values in the table (fig.54).

In allometrical respect of this feature, *Brachyphylla* does not even differ from *Phyllostomus* or *Carollia* (F-value = 1.82 referring to a table value of 3.23 for 95% probability). It is quite interesting that *Lionycteris*, *Lonchophylla* and *Platalina* have the least distances from the outgroup (they all differ with $p < 0.05$ from the outgroup), and *Platalina* remains exactly on the allometric line calculated for *Lonchophylla*. In other words: *Platalina genovensium* represents a large species of *Lonchophylla* also with respect to mandible proportions.

Compared to body size, the phyllonycterines *Erophylla* and *Phyllonycteris* have flattened coronoid processes just as in *Glossophaga*, *Monophyllus*, *Hylonycteris* or *Anoura*. In *Choeroniscus* and *Choeronycteris* (including *Musonycteris*) the flattening of the mandibles is even intensified, though their proportions do match in allometrical respect. There is, however, a striking difference between *Hylonycteris* and *Choeroniscus* (fig.71). As the skull morphology of *Choeroniscus* differs from *Hylonycteris* only by its shovel-like, widened hamuli reaching up to the bullae, there is to be considered whether their function may be related to the extreme flattening of the mandible.

In the course of this study, many species were represented by few specimens. Thus it is impossible to give a comprehensive comparison of intraspecific allometries for the entire group. It does, however, make sense to give an intergeneric comparison of allometric lines between genera comprising numerous individuals and species of distinctly different size. In this respect, the previous systematic reviews suggest to refer to *Lonchophylla*, *Glossophaga*, *Anoura* and *Choeroniscus* apart from the reference genera *Carollia* and *Phyllostomus*. *Erophylla*, *Phyllonycteris* and *Leptonycteris* proved less appropriate, although there were enough specimens available. But the values measured overlap in individual species i.e. in these genera respective intraspecific variability exceeds interspecific distances. Furthermore, differences obtained by measuring are partly found within the error range given by the measuring method.

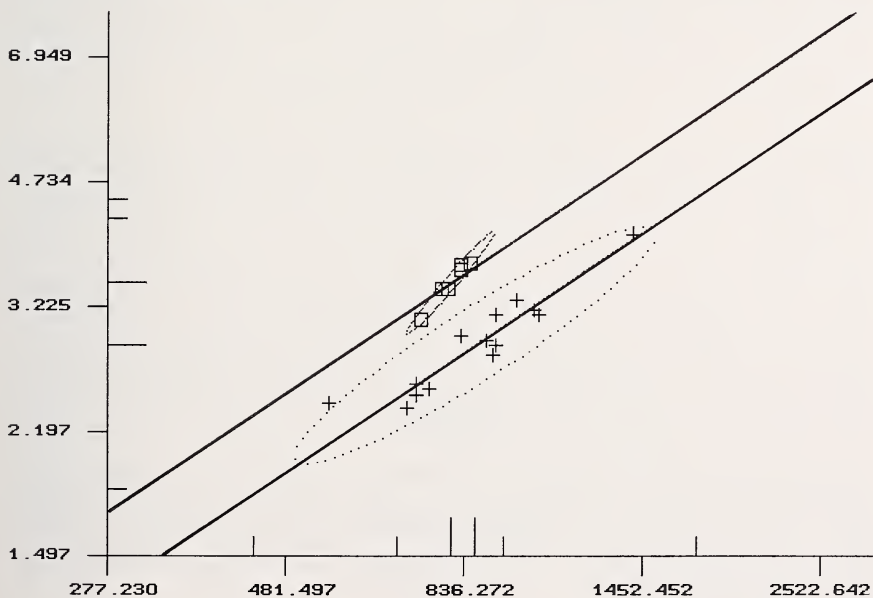


Fig.71: Relation SIZE to coronoid height: comparison between *Hylonycteris* (□) and *Choeroniscus* (+)

Allometrical sex comparison

As already mentioned this comparison can only be performed by random samples of those genera comprising many specimens available. In tab.11 "upper tooth row" (as a regression to the volume measure SIZE) shows for the three genera *Anoura*, *Glossophaga* and *Lonchophylla* that no sex difference could be secured at all.

Instead, there were differences calculated in position and/or gradient in

- *Anoura*: Molar width of the palate ($p < 0.05/p < 0.05$); width of brain case ($p < 0.05/n.s.$); mandible length ($p < 0.05/n.s.$)
- *Choeroniscus*: Molar width of the palate ($p < 0.05/p < 0.05$); width over canini ($p < 0.05/p < 0.05$)
- *Glossophaga*: Coronoid height ($p < 0.05/n.s.$)
- *Lonchophylla*: Mandible length ($p < 0.05/n.s.$)

These arithmetical differences refer to random samples of **genera** comprising many individuals - unfortunately, samples of some **species** are represented by one sex only, for example in *Anoura brevirostrum* (females only). Thus, by means of the material available, no statements can be made on sex-related differences in the studied allometrics.

Allometric conclusions

All this considered, my data give evidence of the following:

In the nectarivorous bats studied here, the proportions of the visceral skull compared to the braincase do not all follow the same allometrics. Five rostrum-related skull measures of the viscerocranium compared to the proportions of the calculated neurocranium volumes, give evidence of different construction principles.

In relative terminal rostral width - measured at the distance of the upper canine teeth - all nectarivorous genera show narrower rostra compared to the genera of the outgroups. The palate surfaces of the Glossophaginae are more (*Choeroniscus*, *Hylonycteris*) or less (*Glossophaga*, *Monophyllus*) rectangular; in *Lionycteris*, *Lonchophylla* but also in *Platalina* the geometry of palate surface tends to be trapezoid. Referring to their allometric gradient only the Lonchophyllinae differ from the outgroup genera.

Three measures (length of the palate, upper tooth row, mandible length) represent rostrum length to a considerable extent. Allometric analysis of all three parameters in proportion to the volume quantity SIZE does not reveal any difference of the Brachyphyllinae (*Brachyphylla*) and Phyllonycterinae (*Erophylla*, *Phyllonycteris*) - classified as basic groups compared to the outgroup (*Carollia*, *Phyllostomus*). Comparing the upper tooth row to SIZE and of the mandible length to SIZE, the genera of the Lonchophyllinae (*Lionycteris*, *Lonchophylla*, *Platalina*) and Glossophaginae (*Anoura*, *Choeroniscus*, *Choeronycteris*, *Glossophaga*, *Hylonycteris*, *Leptonycteris*, *Lichonycteris*, *Monophyllus*, *Musonycteris*) do differ significantly from the outgroup, but they do not differ among each other. There is a remarkably precise correspondence of the measures taken in *Platalina* with the allometrics calculated for *Lonchophylla*.

A clear difference between the genera *Choeroniscus*, *Choeronycteris* and *Hylonycteris* towards the remaining Glossophaginae was revealed by allometric comparison of palate length to the SIZE measure. The allometric regression line (reduced elliptic major axis) shows a transposition (towards a relatively longer palate at equal size), revealing principle differences in skull morphology.

Systematic Conclusions

The systematic relationships in the twelve "glossophagine" genera are discussed for long time:

Based on relative length of metacarpals and phalanges, even Sanborn (1943) classified the Glossophaginae into two groups - *Glossophaga*, *Lichonycteris*, *Scleronycteris*, *Choeroniscus*, *Hylonycteris*, *Choeronycteris* and *Platalina* against *Lonchophylla*, *Leptonycteris*, *Monophyllus*, *Lionycteris* and *Anoura*. These data have to be interpreted, however, mainly in a functional context.

Baker (1967) referred to similarities in the karyotype between *Leptonycteris* and *Glossophaga* with *Phyllostomus*, *Trachops* and *Macrotus* on one hand and *Choeroniscus*, *Choeronycteris* and *Carollia* on the other.

In contrast, Gerber (1968) using immunologic and electrophoretic comparisons of serum proteins, proposed *Choeronycteris* to be closer related to *Phyllostomus* than to *Anoura*, *Glossophaga* and *Leptonycteris*. The latter genera he supposed to be closer relatives of *Carollia*, *Artibeus* and *Sturnira*.

Walton & Walton (1968) who examined shoulder and pelvic girdles, did not find any dichotomy within the Glossophaginae.

Having studied the dentition of the glossophagines, Phillips (1971) presumed that these bats apparently comprised several lines. One of these groups consisted of *Glossophaga*, *Monophyllus*, *Leptonycteris*, *Anoura*, *Lonchophylla*, *Lichonycteris*, *Lionycteris*, *Hylonycteris*, *Scleronycteris* and *Platalina*. This group seemed to be closely related to the phyllostomatine line of *Micronycteris*-*Macrotus* (Smith 1976). The second group of Phillips's comprised *Choeroniscus*, *Choeronycteris* and *Musonycteris*, apparently showing some relationship with the line of *Phyllostomus* within the Phyllostomatinae (Smith 1976). Both groups Phillips characterized by features of the dentition and the skull (c.f. fig.72).

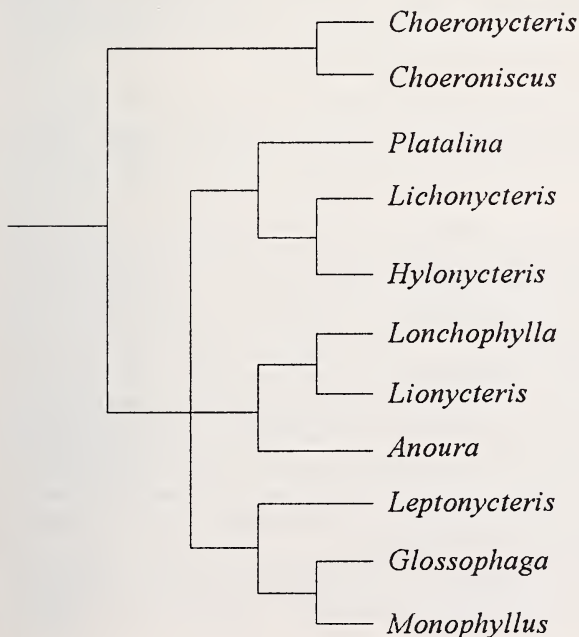


Fig.72: Cladogram of New World nectar-feeding bats adapted from Phillips (1971)

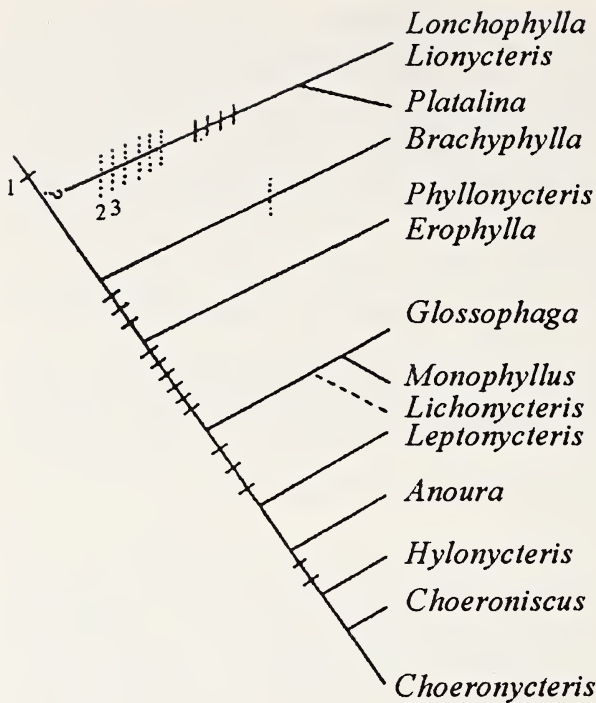


Fig.73: Cladogram of New World nectar-feeding bats adapted from Griffiths (1982)

Based on comparative morphology of the tongue anatomy and the hyoid region ("tunnel insertion of the geniopharyngeus, posterior shift of the styloglossus insertion" in the true Glossophaginae; two lingual arteries in the Lonchophyllinae) Griffiths (1982) proposed that the genera *Lonchophylla*, *Lionycteris*, and *Platalina* must have **separated** at a very early stage from a line of the Brachyphyllinae / Glossophaginae.

At the same time Baker and Hayduk (1982) concluded from chromosome examinations (G-Banding patterns) that the genera separated by Griffiths represent a closely related group **within** the Glossophaginae. Warner (1983) argued with both points of view, emphasizing the difficulties:

In addition to both hypotheses, he proposed a (deliberately artificial) even more "economical" cladistic arrangement. Whereas Griffiths' cladogram (fig.73) required at least seven convergences, Hayduk & Baker (c.f. fig.74) confined themselves to one convergent new development, instead, however, requiring five "retrogressive developments" - all within the group of the "Lonchophyllinae". Warner's cladogram (c.f. fig.75) required three reversions (i.e. features developing retrogressively towards the original condition - all within the "Lonchophyllinae") as well as only two convergences. Thus it would require - theoretically - a minimum of auxiliary hypotheses. Though Griffiths' convergences appear to be the most expensive in numerical terms (7 events), they refer without exception to modifications of the tongue musculature. Similar modifications of the tongue base are also known in other mammalian groups having elongate, protrusible tongues - thus convergent development in both bat groups may be quite probable.

In contrast, the reversions required in Warner's, and especially in Hayduk's & Baker's models, refer to three very special adaptations to nectarivory: "brush-tip of the tongue

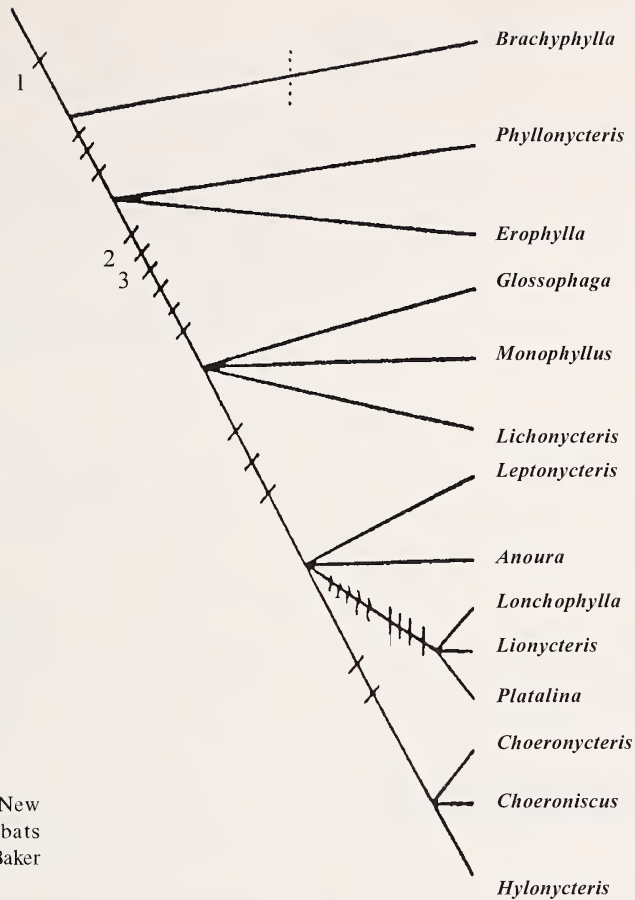


Fig.74: Cladogram of New World nectar-feeding bats adapted from Hayduk & Baker (1982)

covered with hairlike papillae" (1), one single tongue artery present (2) and enlarged tongue venes (3). It is quite improbable that these features - once having developed - were lost again within a group of nectar feeders.

Furthermore, the cladogram of Hayduk & Baker requires additional reversions in the derived features "tunnel insertion of the geniohyoideus" and "back shifting of the insertion of the styloglossus". Presumably the changes at the insertion of these two muscles correspond to the extreme agility of the tongue. As this is a very characteristic feature of nectar feeders, too, it also seems illogical that these characteristics should have been reverted to their original condition within a nectarivorous species group. Exactly matching the point, the authors found that *Lonchophylla* and *Lionycteris* show a wide immunological distance from other nectarivorous New World bats. So, they apparently deviated from the line leading to the Glossophaginae prior to separation of *Brachyphylla*. This supports Griffiths' classification as subfamily "Lonchophyllinae".

Based on this study submitted on skull morphology and allometrics of the measures which characterize rostrum prolongation and which may be recorded craniometrically, the following additional points turned out: 1. *Lionycteris*, *Lonchophylla* and *Platalina* have

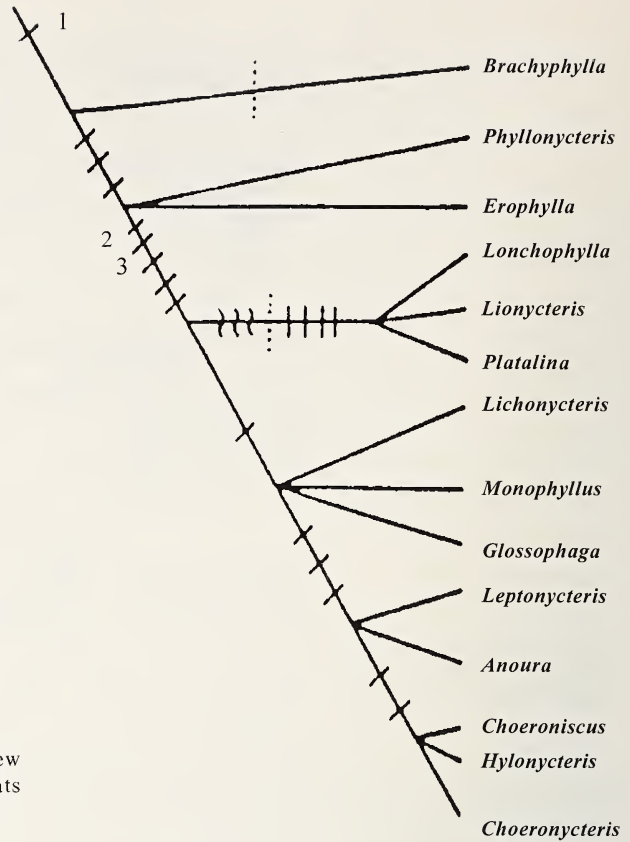


Fig.75: Cladogram of New World nectar-feeding bats adapted from Wamer (1983)

some remarkable features in common: independent from rostral length, all genera lack the zygomatic arches. This derived feature links them with the family Carollinae (genera *Carollia* and *Rhinophylla*) which also always lack bony zygomatic arches.

The dentition shows a strikingly strong development of inner upper incisivi, and the lower ones are always completely preserved. Even here, their features match those of the Carollinae, though probably representing a symplesiomorph condition. The Ramus mandibularis proves quite strong in the allometric analysis (all three genera have the relatively least distance to the outgroup and to *Brachyphylla*) and marks a plesiomorph condition common to all three genera, too.

Referring to size-dependent proportional shift, *Lionycteris*, *Lonchophylla* and *Platalina* correspond to the same allometric constant in the measures examined (width over the canine teeth, coronoid height, length of the maxillar tooth row $C^1 - M^3$, palate length and mandible length). Thus, the relatively longer rostrum of *Platalina* is determined by body size and constructed in accordance with the same principle as *Lionycteris* and *Lonchophylla*.

Considering the cranial characteristics having become available I suggest to include *Platalina genovensium* as the largest species in the genus *Lonchophylla*. The original, very wide gap in size difference compared to the so far known species of *Lonchophylla* which

I suppose will mainly have encouraged Thomas in classifying this species in a genus of its own, is meanwhile linked by *L. handleyi* which Hill described in 1983.

2. *Choeroniscus*, *Hylonycteris* and *Choeronycteris* differ from the remaining Glossophaginae in essential construction principles: with reference to skull morphology, *Choeroniscus* resembles *Hylonycteris* by its airohynchic skull; on the other hand (in contrast to *Hylonycteris*) *Choeroniscus* and *Choeronycteris* share extremely elongate pterygoid processes as well as considerably flatter ramus mandibulares. By allometrical comparison, all three genera give evidence of a transposition of the allometric line in the ratio of SIZE to palate length: although palate length increases with growing total skull length by the same factor as in other Glossophaginae, the allometric line (reduced major axis) runs parallel but on a higher level. So, even in the smaller *Choeroniscus godmani*, relative length of the palate clearly exceeds that of an equal-sized *Lichonycteris*.

Whereas *Hylonycteris* in allometric comparison behaves almost identical to *Choeroniscus* in four of the measures examined (CC, GL, OZR, UKL), allometric analysis of the relation of SIZE to coronoid height reveals a different development of the Ramus mandibularis which would have been overlooked by merely examining the skulls individually. Although, like other Glossophaginae even *Hylonycteris* has a comparatively flat mandible, in *Choeroniscus* and *Choeronycteris* this flattening developed to a more advanced level, distinctly demarcated by the integration constant.

These data on skull morphology and allometry allow to differentiate four predominantly nectarivorous subfamilies within the Phyllostomatidae: these are the Brachyphyllinae and Phyllonycterinae endemic to the Antilles Islands as well as the Lonchophyllinae and Glossophaginae (having been summarized as Glossophaginae by other authors). This systematic subdivision is in accordance with Griffiths (1982).

Within the Glossophaginae sensu strictu the tribe Choeronycterini comprising the genera *Hylonycteris*, *Choeroniscus* and *Choeronycteris* (incl. subgenus *Musonycteris*) represents an extremely high specialized group of nectar feeders.

SUMMARY

Skull morphology of 13 New World nectarivorous bat genera was analyzed under functional aspects and compared with individuals from systematically neighbouring subfamilies of the Phyllostomatidae (Caroliinae, Phyllostominae).

The nectarivorous flower bats are characterized by special adaptations to this diet, primarily imposing cranially by rostral prolongation to various extent. The degree of this prolongation varies considerably within and between individual genera and can be judged as an evidence of the extent of feeding specialization. Species taking varied diet (*Glossophaga*, *Lionycteris*) have shorter jaws than highly specialized nectar feeders (*Choeronycteris*) whose palate length reaches half the total skull length. These proportions are, however, also influenced by body size: small species possess relatively larger braincases and shorter jaw lengths, larger specimens relatively smaller braincases and longer jaws, respectively.

By means of 17 measures, skull proportions as well as their allometric conditions (gradient of their reduced major axes, integration constants) were compared among the genera examined (total number of specimens: 265).

As a reference quantity for individual measures, a calculated volume measure - SIZE - was chosen, representing the braincase.

By allometrical comparison of the measures related to feeding apparatus (width of the palate over the canini, palate length, upper tooth row, mandible length, height of the coronoid process) the following points turned out:

Generally, the various development of rostrum prolongation cannot be characterized by distinctly distinguishable construction principles. It is, rather, affected by the allometric and integration constants which are established for the entire group.

In contrast, in the genera *Choeroniscus*, *Hylonycteris* and *Choeronycteris* the length of the palate shows a transposition of the allometric line deviating from the condition of the remaining Glossophaginae. This represents another principle of construction proving the close relationship of all three genera. The systematic separation of the subfamily - formerly summarized in a single taxon - into Glossophaginae and Lonchophyllinae according to morphological criteria of the soft parts (Griffiths 1983) is also supported by the cranial data of this study (lacking zygomatic arches, incisors, mandibular shape).

Furthermore, the allometric data allow to classify *Platalina genovensium* as a large species within the the genus *Lonchophylla*.

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- & — (1985): *Glossophaga mexicana*. — Mammalian Species 245:1-2.
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APPENDIX

Material examined

Phyllostomatinae

Phyllostomus discolor:

BMNH 5.5.22.1, -, Ecuador

Phyllostomus elongatus:

MNHUB 3217, ♀, Suriname, leg. A. Kappler

MNHUB 3359, ♂, Suriname, leg. A. Kappler

MNHUB 3985, ♂, Suriname, leg. A. Kappler

MNHUB 3985(a), ♀, Suriname, leg. A. Kappler

MNHUB 4185, ♂, Berg an Dal, Suriname, leg. Mösche

Phyllostomus hastatus:

BMNH 14.9.1.17, ♀, Sierra de Carabobo, Venezuela

MNHUB "--", ♂, St. Pablo, leg. G. Hopke, 6.3.1897

MNHUB 59, -, Bolivia, leg. Steinbach A.11.09

MNHUB 158, -, Bolivia, leg. Steinbach A.11.09

MNHUB 2592, ♂, Brazil, Parreys

MNHUB 10025, -, Brazil, leg. Posnansky

MNHUB 37387, -, Para, Brazil, leg. Otto Bertram

SMF 25475, no data

Carollinae

Carollia castanea:

SMF 41994, ♂, Villavicencio, Colombia, leg. H. Stephan, 1971

SMF 41995, ♀, Villavicencio, Colombia, leg. H. Stephan, 1971

SMF 43027, ♂, Finca el Buque, Villavicencio, Colombia, leg. E. Thiery, 1979

SMF 45690, ♀, Lagao del Calado, Manaus, Brazil, leg. F. Reiss, 1971

SMF 54902, ♂, Apulo, Cundinamarca, Colombia, leg. E. Patzelt, 1982

ZIM (SO) 5, ♀, Rio Cuyabeno, Ecuador, leg. E. Patzelt, 1982

Carollia perspicillata:

MEPN 1106, ♂, Rio Pastaza, Ecuador, leg. Spillmann

MEPN 1176, -, leg. Spillmann

MEPN 3024, ♂, Cerro Guataraco, Ecuador, leg. Spillmann, 24.11.1930

MEPN 3284, ♂, Sto. Domingo de los Colorados, Ecuador, leg. Spillmann

MEPN 3285, ♀, Esmeraldas, Ecuador, leg. Spillmann

MEPN 3292, ♀, Cerro Guataraco, Ecuador, leg. Spillmann, 12.9.1932

MEPN 8027, -, San Lorenzo, Esmeraldas, Ecuador, leg. L. Albuja, 16./17.2.1980

MEPN 8142, ♀, Rio Palenque, Ecuador, leg. L. Albuja, 28.4.1981

MEPN 8144, -, Rio Palenque, Ecuador, leg. L. Albuja, 28.4.1981

MEPN 8147, -, Rio Palenque, Ecuador, leg. L. Albuja, 29.10.1981

MEPN 33101, ♂, Avila, Mangayacu, Ecuador, leg. Spillmann, 1939

SMF 15655, ♀, Panama, leg. I. Eibl-Eibesfeld

SMF 15656, -, Panama, leg. I. Eibl-Eibesfeld

SMF 15657, -, Panama, leg. I. Eibl-Eibesfeld

SMF 18748, ♀, Cueva de Ganango, Venezuela, 27.1.1952

SMF 18751, no data

- SMF 43022, ♂, Finca el Buque, Villavicencio, Meta, Colombia, leg. E. Thiery, 15.5.1979
 SMF 43023, ♂, Finca el Buque, Villavicencio, Meta, Colombia, leg. E. Thiery, 1979
 SMF 43024, ♂, Finca el Buque, Villavicencio, Meta, Colombia, leg. E. Thiery, 1979
 SMF 43025, ♀, Finca el Buque, Villavicencio, Meta, Colombia, leg. E. Thiery, 1979
 SMF 43026, ♀, Finca el Buque, Villavicencio, Meta, Colombia, leg. E. Thiery, 15.5.1979
 SMF 66381, ♂, Hacienda la Pacifica Cabas, Guanacaste, Costa Rica, leg. Küsten & Joermann, 8.10.1981

Carollia subrufa:

- AMNH 97516, -, Barillos, Guatemala
 AMNH 235304, ♂, Santa Rosa, 6 km N Avellana, Guatemala
 AMNH 235716, ♀, Santa Rosa, Guatemala
 AMNH 235717, ♀, Santa Rosa, Guatemala
 AMNH 235721, ♀, Santa Rosa, Guatemala
 AMNH 235725, ♂, Santa Rosa, Guatemala
 AMNH 235726, ♀, Santa Rosa, Guatemala

- AMNH 243759, ♀, Tutiapa, El Paraiso, Guatemala
 AMNH 230500, ♂, Oxapampa, Peru, leg. M.G. Tuttle, 25.7.1954

Rhinophylla pumila:

- AMNH 262470, -, Aqua dulce, Pando, Bolivia, leg. A.W. Dickermann, 22.7.1986

Rhinophylla fischeriae:

- AMNH 230481, ♂, Dept. Pasco, Prov. Oxapampa, Peru, leg. D.L. Knowlton, 23.7.1964
 AMNH 230482, ♂, Oxapampa, Peru, leg. K.R. Stringer, 7.7.1964
 AMNH 230483, ♂, Oxapampa, Peru, leg. K.R. Stringer, 7.7.1964
 AMNH 230496, ♀, Oxapampa, Peru, leg. D.L. Knowlton, 25.7.1964
 AMNH 230498, ♂, Oxapampa, Peru, leg. D.L. Knowlton, 25.7.1964
 AMNH 230499, ♀, Oxapampa, Peru, leg. K.R. Stringer, 22.7.1964
 AMNH 230500, ♂, Oxapampa, Peru, leg. M.D. Tuttle, 25.7.1954

Brachyphyllinae

Brachyphylla cavernarum (= *B. minor*):

- AMNH 149366, ♂, Barbados
 AMNH 149367, ♂, Barbados
 AMNH 213898, ♀, Barbados
 BMNH 18.4.1.11, -, Antigua

Brachyphylla nana (= *B. pumila*):

- AMNH 97597, ♂, Dominican Republic
 AMNH 214390, ♂, Dominican Republic
 AMNH 244914, ♂, Dominican Republic
 BMNH 52.588, ♀, Haiti
 BMNH -, ♂, Cuba
 ROM 45708, -, Los Patos, Dominican Republic
 ZFMK 77.651, -, Cuba

Phyllonycterinae

Erophylla bombifrons:

- AMNH 39339, ♂, Pueblo Viejo, Porto Rico, 5.7.1916
 AMNH 39340, ♂, Pueblo Viejo, Porto Rico, 5.7.1916
 AMNH 39341, ♀, Pueblo Viejo, Porto Rico, 5.7.1916
 AMNH 39345, ♂, Pueblo Viejo, Porto Rico, 6.7.1916
 ROM 42754, ♀, Corozál, Puerto Rico
 ROM 42755, ♀, Corozál, Puerto Rico
 ROM 44552, ♂, Aguas Buenas, Puerto Rico
 ROM 45709, ♀, Fantina, Dominican Republic
 ROM 45710, ♂, Fantina, Dominican Republic
 ROM 45711, ♀, Fantina, Dominican Republic
 USNM 252618, ♀, San Michel, Haiti, leg. A.J. Poole, 11.3.1928
 USNM 252619, ♀, San Michel, Haiti, leg. A.J. Poole, 11.3.1928
 USNM 253634, ♀, San Michel, Haiti, leg. Poole & Perrygo, 23.12.1928

Erophylla sezekorni:

- AMNH 41056, ♂, Siboney, Cuba, 26.2.1917
 AMNH 41057, ♂, Siboney, Cuba, 26.2.1917
 AMNH 41059, ♂, Siboney, Cuba, 26.2.1917
 AMNH 41066, ♀, Siboney, Cuba, 26.2.1917
 AMNH 41067, ♀, Siboney, Cuba, 26.2.1917
 AMNH 41069, ♀, Siboney, Cuba, 26.2.1917
 ROM 63164, ♂, Cueva de Gabairo, C39, Cuba
 ROM 63165, ♂, Cueva de Gabairo, Cuba
 ROM 63166, ♂, Cueva de Gabairo, Cuba
 USNM 538180, ♂, Cayman Brac West End, 3.5km NE near South East Bay, Cayman Is., leg. G.S. Morgan, 30.7.1979
 USNM 538181, ♂, Cayman Is., leg. G.S. Morgan, 30.7.1979
 USNM 538182, ♂, Cayman Is., leg. G.S. Morgan, 30.7.1979
 USNM 538183, ♀, Cayman Is., leg. G.S. Morgan, 30.7.1979
 USNM 538184, ♀, Cayman Is., leg. G.S. Morgan, 30.7.1979
 USNM 538185, ♀, Cayman Is., leg. G.S. Morgan, 30.7.1979

Phyllonycteris poeyi:

- ROM 63170, ♂, Cueva de los Majaes, Siboney, 14km C39, Cuba
 ROM 63171, ♂, Cueva de los Majaes, Siboney, 14km C39, Cuba
 ROM 63172, ♂, Cueva de los Majaes, Siboney, 14km C39, Cuba
 ROM 37069, FEM
 ROM 37070, M
 ROM 37071, ♀, St. Claire Cave, Ewarton, 2mls. S St. Catherine Parish, Jamaica
 SMF 12139, ♀, Cuba, don. Berlin
 ZFMK 77.649, Cuba, leg. Gundlach

Lonchophyllinae

Lionycteris spurrelli:

- AMNH 97220, ♂, Mocajuba, Rio Tocantins, Brazil, leg. Ollalla Bros., 15.11.1931
 AMNH 97222, ♂, Mocajuba, Rio Tocantins, Brazil, leg. Ollalla Bros., 15.11.1931
 AMNH 97224, ♀, Mocajuba, Rio Tocantins, Brazil, leg. Lalla Bros., 16.11.1931
 AMNH 97261, ♂, Mocajuba, Rio Tocantins, Brazil

AMNH 230207, ♀, Peru
 AMNH 230209, ♀, Peru
 AMNH 239891, ♂, Peru
 AMNH 260004, ♀, Venezuela
 BMNH 69.392, ♂, Guayana
 BMNH 13.8.10.1 (**Type**), ♂, Condoto Choko, Colombia, leg. Spurrell
 MHNG 1682.83, ♀, Jumandi, 10km N Archidona, Napo, Ecuador, leg. J. Garzoni, 1982

Lonchophylla thomasi:

AMNH 97272, ♀, Brazil
 AMNH 210688, ♀, Bolivia
 AMNH 230281, ♂, Peru
 AMNH 230282, ♀, Peru
 BMNH 65.633, ♂, British Guayana
 BMNH 69.1278, ♂, Araenga, Para, Brazil
 BMNH 69.1280, ♀, Araenga, Para, Brazil
 MEPN 2018, -, Sinolotor, Ecuador, leg. Spillmann
 MEPN 80265, ♂, Urbina, Esmeraldas, Ecuador, leg. L. Albuja, 16.2.1980
 JK 30, -, Peru, leg. J. Koepke
 JK 66, -, Peru, leg. J. Koepke
 JK 278, -, Peru, leg. J. Koepke
 RMNH 30, ♂, leg. J.A. Allen, 1904
 RMNH 69, ♂, leg. J.A. Allen, 1904
 RMNH 17346, ♂, Marowijne, Nassaugebergte, Suriname, leg. Surinam Exp., 25.2.1949
 RMNH 17347, FEM. Marowijne, Nassaugebergte, Suriname, 25.2.1949

Lonchophylla mordax:

BMNH 3.9.5.31, ♂, Lamarão, Bahia, leg. O. Thomas
 BMNH 3.9.5.32, ♂, Lamarão, Bahia, leg. O. Thomas
 BMNH 3.9.5.33, ♂, Lamarão, Bahia, leg. O. Thomas
 BMNH 3.9.5.34, (**Type**), ♂, Lamarão, Bahia, leg. O. Thomas
 BMNH 3.9.5.35, ♂, Lamarão, Bahia, leg. O. Thomas
 BMNH 3.9.5.36, -, Lamarão, Bahia, leg. O. Thomas
 MEPN 7463, ♀, Boca del Rio Lito, Ecuador, leg. G. Herrera, 3.6.197?

Lonchophylla robusta:

BMNH 78.1354, ♀, Yaupi, Morona, Prov. Santiago, Ecuador
 BMNH 78.1355, ♀, Yaupi, Morona, Prov. Santiago, Ecuador
 BMNH 78.1356, ♀, Yaupi, Morona, Prov. Santiago, Ecuador
 BMNH 78.1357, ♀, Yaupi, Morona, Prov. Santiago, Ecuador
 BMNH 78.1358, ♀, Yaupi, Morona, Prov. Santiago, Ecuador
 BMNH 78.1359, ♀, Yaupi, Morona, Prov. Santiago, Ecuador
 BMNH 78.1360, ♀, Yaupi, Morona, Prov. Santiago, Ecuador
 BMNH 78.1361, ♀, Yaupi, Morona, Prov. Santiago, Ecuador
 BMNH 78.1362, ♀, Yaupi, Morona, Prov. Santiago, Ecuador (2° 93'S, 77° 54'W)
 MEPN 80214, ♂, San Lorenzo, Prov. Esmeraldas, Ecuador, leg. L. Albuja
 MEPN 80464, -, Barragantete, Ecuador, leg. L. Albuja

Lonchophylla handleyi:

BMNH 81.174, ♀, Los Tayos, Morona, Prov. Santiago, Ecuador (3° 07'S, 78° 12'W), leg. J.E. Hill
 BMNH 78.1363, ♂, Los Tayos, Morona, Prov. Santiago, Ecuador, leg. J.E. Hill

BMNH 78.1364, ♂, Los Tayos, Morona, Prov. Santiago, Ecuador, leg. J.E. Hill
 BMNH 78.1365, ♀, Los Tayos, Morona, Prov. Santiago, Ecuador, leg. J.E. Hill
 BMNH 78.1366, ♂, Los Tayos, Morona, Prov. Santiago, Ecuador, leg. J.E. Hill
 BMNH 78.1367, ♀, Los Tayos, Morona, Prov. Santiago, Ecuador, leg. J.E. Hill
 BMNH 78.1368, **(Type)**, ♀, Los Tayos, Morona, Prov. Santiago, Ecuador, leg. J.E. Hill
 BMNH 78.1369, ♂, Los Tayos, Morona, Prov. Santiago, Ecuador, leg. J.E. Hill
 BMNH 78.1370, ♂, Los Tayos, Morona, Prov. Santiago, Ecuador, leg. J.E. Hill
 BMNH 78.1371, ♀, Los Tayos, Morona, Prov. Santiago, Ecuador, leg. J.E. Hill
 BMNH 78.1372, ♂, Los Tayos, Morona, Prov. Santiago, Ecuador, leg. J.E. Hill
 BMNH 78.1374, ♀, Los Tayos, Morona, Prov. Santiago, Ecuador, leg. J.E. Hill
 BMNH 78.1375, ♀, Los Tayos, Morona, Prov. Santiago, Ecuador, leg. J.E. Hill
 BMNH 78.1376, ♀, Los Tayos, Morona, Prov. Santiago, Ecuador, leg. J.E. Hill
 BMNH 78.1377, ♂, Yaupi, Morona, Ecuador
 BMNH 78.1378, ♀, Yaupi, Morona, Ecuador

Platylina genovenstium:

AMNH 257108, ♂, Peru
 BMNH 27.11.1938 **(Type)**, ♂, Lima, Peru, leg. Esposto
 NHMB 10.623, ♀, Angolo, Peru, leg. W. Markl, 1957

Glossophaginae

Glossophaga comissarisi:

BMNH 67.799, ♀, Bonanza, Nicaragua, leg. J. KnoxJones jr., 29.2.1964
 BMNH 94.3.30.3, -, Nicaragua
 SMF 11981, -, Marajo, Brazil, leg. W. Ehrhardt, 1.10.1923
 SMF 12185, ♂, Marajo, Brazil, leg. W. Ehrhardt, 16.11.1923
 SMF 12192, ♂, Marajo, Brazil, leg. W. Ehrhardt, 10.10.1923
 SMF 13396, ♂, Hacienda Chilata, Sonsonate, El Salvador, leg. H. Felten, 28.6.1953
 MEPN 79852, -, Limoncocha, Napo, Ecuador, leg. L. Albuja, 8.1979
 MHNG 1682.88, ♂, Momotombo, cité géothermique, Nicaragua, leg. Chambrier-Jaccoud, 4.2.1983

Glossophaga longirostris:

BMNH 11.5.25.83, ♂, San Estevan, Venezuela, leg. S.M. Klages
 BMNH 11.5.25.84, ♂, San Estevan, Venezuela, leg. S.M. Klages
 BMNH 11.5.25.85, ♂, San Estevan, Venezuela, leg. S.M. Klages
 BMNH 11.5.25.86, ♀, San Estevan, Venezuela, leg. S.M. Klages
 BMNH 11.5.25.87, ♀, San Estevan, Venezuela, leg. S.M. Klages
 BMNH 27.11.19.25, ♀, Curacao
 BMNH 52.8.12.11, ♀, St. Vincent
 BMNH 91.5.15.8, ♂, Mustique
 BMNH 96.11.8.5, ♀, Grenada
 MEPN 3294, -, Esmeraldas, Ecuador, leg. Spillmann
 MEPN 3295, -, Esmeraldas, Ecuador, leg. Spillmann
 MEPN 3296, -, Esmeraldas, Ecuador, leg. Spillmann
 MEPN 3297, -, Esmeraldas, Ecuador, leg. Spillmann
 MEPN 80417, ♂, Borriganete, Ecuador, leg. L. Albuja
 MEPN 80419, -, Borriganete, Ecuador, leg. L. Albuja, 1.4.1980
 MHNG 1057.24, ♀, Girardot, Cundinamarca, Columbia, leg. Valdivieso, 1961
 MHNG 1682.90, ♀, Tolu, Bolivar, Columbia, leg. Mechler, 16.4.1965
 RMNH 12227, ♀, Tobago, Trinidad, leg. G.F. Mees, 13.2.1954

RMNH 12228, ♀, Tobago, Trinidad, leg. G.F. Mees, 22.3.1954
 RMNH 12239, ♀, Grafton, Tobago, Trinidad, leg. G.F. Mees, 1954
 RMNH 12242, ♀, Grafton, Tobago, Trinidad, leg. G.F. Mees, 13.2.1954
 RMNH 14359, ♀, Los Testigos, leg. P.W. Hummelinck, 1936
 RMNH 14388, ♂, Aruba, leg. P.W. Hummelinck, 4.10.1945
 RMNH 14389, ♀, Curacao, leg. P.W. Hummelinck, 26.9.1948
 RMNH (14390), ♀, Curacao, leg. P.W. Hummelinck, 26.9.1948
 RMNH 14722, -, Aruba, 1.10.1945, don. Van Pijl, 1945
 RMNH 14724, ♀, Curacao, 10.1.1946

Glossophaga leachii ("G. alticola"):

BMNH 67.800, ♂, Managua, Nicaragua, leg. A.A. Alcom, 14.6.1956
 SMF 13457, ♂, Finca Raquelina, Ahuachapán, El Salvador, leg. H. Felten, 2.7.1953
 SMF 15078, ♂, Hacienda San Antonio, Sonsonate, leg. H. Felten, 12.11.1953

Glossophaga morenoi (= *mexicana*):

AMNH 167474, -, Mexico
 AMNH 171259, -, Mexico
 AMNH 167481, -, Mexico
 AMNH 185083, -, Mexico
 AMNH 189210, -, Mexico

Glossophaga soricina:

ZIM (SO) 10, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 11, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 12, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 13, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 14, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 15, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 16, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 17, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 18, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 19, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 20, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 21, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 22, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 26, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 28, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 29, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 30, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 31, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 33, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 34, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 35, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 36, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 39, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 42, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 ZIM (SO) 80, -, Hacienda el Timbre, Esmeraldas, Ecuador, leg. E. Patzelt, 1982
 BMNH 39119, no data
 BMNH 1.11.3.14, ♀, Rio Jordao, Brazil
 BMNH 1.11.3.15, ♀, Rio Jordao, Brazil

- BMNH 1.11.3.18, ♀, Brazil
 BMNH 3.7.1.162, ♀, Ipanema, Sao Paulo, Brazil
 BMNH 11.12.22.5, ♀, Sn. Amazons., Brazil
 BMNH 11.12.22.6, ♀, Rio Yumundá, Sn. Amazons., Brazil
 BMNH 24.2.4.5, ♀, Caldeirao, Marajo, Amazon., Peru
 BMNH 28.5.2.130, ♀, Chicosa Loreto, Peru
 BMNH 66.4394, ♀, San José, Costa Rica
 BMNH 67.798, ♂, San Antonio, Chinandega, Nicaragua
 BMNH 88.8.8.27, -, Tabasco
 MEPN 1445, ♀, Isla Silva, Prov. Guayas, Ecuador
 MEPN 8024, ♀, San Lorenzo, Esmeraldas, Ecuador, leg. L. Albuja, 16.2.1980
 MEPN 47109, -, Chontillal, Ecuador, leg. E. Patzelt, 27.11.1974
 MEPN 78104, ♀, San Pedro de los Catanes, 28km via Lago Agrio, Ecuador, leg. R. Nevarrete, 5.10.1978
 MEPN 791123, ♂, Jumandi, Prov. Napo, Ecuador, leg. L. Albuja, 3/5.12.1979
 MHNG 1061.61, ♂, Mallares/Sullana, Peru, leg. Kramer & Markl, 3.1957
 MHNG 1682.79, -, Villarica, Paraguay
 MHNG 1682.84, ♂, Atacames, Sua, Ecuador, leg. J. Garzoni, 1982
 MHNG 1682.85, ♀, Santa Rosa, Mun. Vigia, Pará, Brazil, leg. Novaes Souza (M. Goeldi), 1972
 MHNG 1682.86, ♀, Arroyo Tagatya-mi, 25km E de Puerto Max, Conception, Paraguay, leg. Weber, 1983
 MHNG 1682.87, ♀, Momotombo, cité geothermique, Nicaragua, leg. Chambrier Jaccoud, 1983
 MHNG 1682.89, -, Escazu, Costa Rica, leg. C.F. Underwood, 23.7.1898
 M781 (Kopenhagen), ♀, Realejo, Oersted, 1949
 M782 (Kopenhagen), ♂, no data
 M2983 (Kopenhagen), ♂, Caldurao, Marajo, 1923
 M2984 (Kopenhagen), ♀, Aruba, ded. 13.8.1968
 L13 (Kopenhagen), no data
 RMNH 34373, ♂, Matta, Suriname, 11.1.1963
 RMNH 34374, ♀, Nickerie, Suriname, leg. D.G. Reeder, 19/20.5.1981
 ZFMK 80.11, ♂, Orocué, 5.1897, ex Coll. Mus. Göttingen, Bürger coll. 1978
 ZFMK 8075, ♀, Puerto Maldonado, Rio Madre de Dios, Peru, leg. E. Lenkenhoff, 8.1980
 ZFMK 67194, ♂, Mato Grosso, Brazil
 ZFMK 67195, ♀, Mato Grosso, Brazil
 ZFMK 80865, ♂, Puerto Maldonado, Rio Madre de Dios, Peru, leg. E. Lenkenhoff, 1980
 ZFMK 80868, ♂, Puerto Maldonado, Rio Madre de Dios, Peru, leg. E. Lenkenhoff, 1980
 ZFMK 80869, ♂, Puerto Maldonado, Rio Madre de Dios, Peru, leg. E. Lenkenhoff, 1980
 ZFMK 80870, ♀, Puerto Maldonado, Rio Madre de Dios, Peru, leg. E. Lenkenhoff, 1980
 ZFMK 80876, ♀, Puerto Maldonado, Rio Madre de Dios, Peru, leg. E. Lenkenhoff, 1980
 ZFMK 80877, ♀, Puerto Maldonado, Rio Madre de Dios, Peru, leg. E. Lenkenhoff, 1980
 ZFMK 811502, ♂, Rio Tambopata, Peru, leg. E. Lenkenhoff, 1981
 NHMW 21362, ♀, Huanaco, Peru, leg. G. Paetzmman, 1976

Monophyllus plethodon (incl. *M. luciae*):

- BMNH 18.4.1.7, ♂, Antigua
 BMNH 18.4.1.8, ♂, Antigua
 BMNH 18.4.1.9, ♂, Antigua
 BMNH 32.4.1.11, ♀, Domenica
 RMNH 17854, ♀, Dark Cave, Barbuda, Lesser Antilles, leg. P.W. Hummelinck, 6.7.1955

Monophyllus redmani:

- BMNH --, -, Jamaica
 BMNH 65.3996, -, Jamaica
 BMNH 7.1.1.666, -, Jamaica
 BMNH 7.1.1.667, -, Jamaica
 BMNH 7.1.1.668, -, Jamaica
 BMNH 75594, ♂, Ewarton, St. Cath. Parish, (Googwin), Jamaica
 MHNG, 982.93, ♀, Jamaica, leg. C.F. Underwood
 SMF 57976, ♀, St. Claire Cave, Ewarton, St. Catharine Parish, Jamaica, leg. Goodwin, 29.12.1965
 SMF 57977, ♀, St. Claire Cave, Ewarton, St. Catharine Parish, Jamaica, leg. Goodwin, 29.12.1965
 SMF 57978, ♂, St. Claire Cave, Ewarton, St. Catharine Parish, Jamaica, leg. Goodwin, 29.12.1965
 ZFMK 82270, ♂, Green Hills, Blue Mountains (1200m asl), Jamaica, leg. H.H. Wii, 1982

Lichonycteris degener (incl. *L. obscura*):

- AMNH 95118, ♀, Brazil
 AMNH 95485, ♀, Brazil
 AMNH 131769, -, Costa Rica
 BMNH 3.4.5.36, ♀, Cayenne, Fr.-Guayana, leg. O. Thomas
 BMNH 95.4.29.1 (**Type**), ♀, Managua, Nicaragua, leg. D. Rothschuh
 BMNH 96.10.1.20, -, San José, Costa Rica, leg. C.F. Underwood
 MEPN 741050, ♀, Rio Palenque, Ecuador, leg. B. Stott & K. Mioyota
 MHNG 1682.82, ♂, Santarem, Rio Solimoens, Amazonas, Brazil, leg. P. Pictet, 1957

Leptonycteris nivalis (incl. *L. curasoae*):

- BMNH 631811, ♂, Jalisco, Mexico, leg. A.C. Buller
 BMNH 66.6040, -, Jalisco, Mexico, leg. A.C. Buller
 BMNH 70.2057, ♀, Cuevas del Guano, Falcon, Venezuela
 BMNH 70.2058, ♂, Cuevas del Guano, Falcon, Venezuela
 BMNH 93.5.7.9, ♂, Jalisco, Mexico
 BMNH 93.5.7.10, M. Tizapan el Alto, Jalisco, Mexico, leg. A.C. Buller
 BMNH 93.5.7.11, M. Tizapan el Alto, Jalisco, Mexico, leg. A.C. Buller
 MHNG 1682.78, -, Columbia
 RMNH 14394, ♂, Cueba Bosá, leg. P.W. Hummelinck, 1949
 RMNH 14395, ♂, Cueba Bosá, leg. P.W. Hummelinck, 7.3.1949
 RMNH 14396, ♂, Cueba Bosá, leg. P.W. Hummelinck, 1949
 RMNH 14397, ♂, Cueba Bosá, leg. P.W. Hummelinck, 7.3.1949
 RMNH 14398, ♀, Cueba Bosá, leg. P.W. Hummelinck, 7.3.1949
 RMNH 14717, ♂, Cueba di Watapana, Lima, Bonaire, leg. P.W. Hummelinck, 1954
 1068 (Museum Kopenhagen). ♂, Jalisco, Mexico
 1069 (Museum Kopenhagen). ♂, Jalisco, Mexico, leg. Buller, 1893, ex Coll. Brit.Mus.
 SMF 37780, ♀, Rancho las Margaritas, Mexico, leg. Greenhall & Schmidt, 25.4.1969
 SMF 37781, -, Rancho las Margaritas, Mexico, leg. Greenhall & Schmidt, 25.4.1969
 SMF 37782, -, Rancho las Margaritas, Mexico, leg. Greenhall & Schmidt, 1969

Leptonycteris yerbabuena (= *sanborni*):

- AMNH 208226, ♂, Oaxaca, Mexico
 AMNH 208227, ♂, Oaxaca, Mexico

AMNH 213763, ♂, Oaxaca, Mexico

MHNG 1184.11, ♂, Chiapas, 7mls WSW Ocozocautle, Mexico, leg. Carter, 1962

Anoura caudifer:

SMF 69747, ♀, 15km SE St. Laurent, Fr.-Guayana, leg. D. Kock & H. Stephan, 29.10.1985

SMF 69749, ♀, 15km SE St. Laurent, Fr.-Guayana, leg. D. Kock & H. Stephan, 29.10.1985

SMF 69750, ♀, 15km SE St. Laurent, Fr.-Guayana, leg. D. Kock & H. Stephan, 29.10.1985

MHNG 1682.80, ♂, Mera, Pastaza, Ecuador, 12.3.1981

RMNH 34379, ♂, Brownsberg, Distr. Brokopondo, Suriname, leg. G.F. Mees, 28.2.1972

RMNH 17269, ♀, San Miguel Paulista, Sao Paulo, Brazil, leg. E. Deute, 2.10.1960

RMNH 13487, ♀, Jodensavanne, Suriname, leg. J. Lindenau, 1954

ZFMK 59.55, ♀, Rio Bobonaza, Ecuador, 10.1.1959

ZFMK 59.56, ♀, Rio Bobonaza, Ecuador, 10.1.1959

MEPN 791127, ♀, Cueva di Archidona, Jumandi, Ecuador, leg. L. Albuja, 4.10.1979

JK 219, ♀, Peru, leg. J. Koepke

"Lonchoglossa", Juli 1982

L-17 (Museum Kopenhagen), no data

L-18 (Museum Kopenhagen), no data

Anoura cultrata (=brevirostrum, =wercklae):

AMNH 214324, ♀, Peru

AMNH 233250, ♀, Peru

AMNH 233251, ♀, Peru

AMNH 233252, ♀, Peru

AMNH 233253, ♀, Peru

AMNH 233254, ♀, Peru

AMNH 233255, ♀, Peru

AMNH 233262, ♀, Peru

AMNH 233263, ♀, Peru

AMNH 233268, ♀, Peru

Anoura geoffroyi:

RMNH 16416, ♂, Tafelberg, Suriname, leg. D.C. Geyskes, 1958, det. Husson

RMNH 17851, ♀, Tamana Bat Cave, Trinidad, leg. P.W. Hummelinck, 8.1.1955

RMNH 17853, ♂, Tamana Bat Cave, 230m asl, Trinidad, leg. P.W. Hummelinck, 8.1.1955

RMNH 34375, ♀, Katalabo, Nickerie, Suriname, leg. D.G. Reeder, 3.5.1981

SMF 69766, ♂, Kourou, Fr.-Guayana, leg. D. Kock & H. Stephan, 13.11.1985

SMF 69767, ♂, Savanne le Gallion, 23km S Cayenne, Fr.-Guayana, leg. D. Kock & H. Stephan, 13.11.1985

MEPN 1126, -, Bocas del Cerro, Saloya, Ecuador, leg. Spillmann, 4. 1939

MEPN 1127, ♂, Bocas del Cerro, Saloya, Ecuador, leg. Spillmann, 4. 1939

MEPN 7941, ♂, Piedro Blanca, Rumirahui, Ecuador, leg. L. Albuja, 15.4.1979

MEPN 7942, ♂, Piedro Blanca, Rumirahui, Ecuador, leg. L. Albuja, 15.4.1979

MEPN 3948, ♂, Rio Saloya, Bocas del Cerro, Saloya, Ecuador, leg. Spillmann, 4. 1939

MEPN 3949, ♂, Rio Saloya, Bocas del Cerro, Saloya, Ecuador, leg. Spillmann, 4. 1939

MEPN 6762, -, Esmeraldas, Ecuador, -

MEPN 39411, -, Rio Saloya, Bocas del Cerro, Saloya, Ecuador, leg. Spillmann, 1939

NHMW 30720, ♀, Campinas, 22 54'S/47 06'W, Sao Paulo, Brazil, leg. C. Vanzolini, 1906

MHNG 1682.81, ♀, Mera, Pastaza, Ecuador, 18.11.1981

ZIM (SO) 187, ♀, San Antonio de Pichincha, Quito, Ecuador, leg. E.H. Solmsen, 7. 1983

ZIM (SO) 198, ♀, San Antonio de Pichincha, Quito, Ecuador, leg. E.H. Solmsen, 7. 1983
 ZIM (SO) 199, -, San Antonio de Pichincha, Quito, Ecuador, leg. E.H. Solmsen, 7. 1983
 ZIM (SO) 201, ♀, San Antonio de Pichincha, Quito, Ecuador, leg. E.H. Solmsen, 7. 1983

Anoura latidens:

AMNH 261230, ♀, Terr. Fed. Amazonas, Venezuela, leg. R.W. Dickerman, 14.4.1984

Anoura wiedii:

BMNH 27.11.1928, ♂, Campinas, Brazil
 BMNH 27.11.1929, ♂, Brazil
 BMNH 27.11.1930, ♀, Brazil
 BMNH 27.11.1931, ♀, Brazil
 BMNH 27.11.1932, ♀, Brazil
 RMNH 25482, ♂, Campina, Estado de Sao Paulo, Brazil, leg. Vangolini & G. Doria, 1906
 793 (Museum Kopenhagen), ♀, Lagoa Santa, Brazil, leg. Reinhardt, 27.8.1955
 792 (Museum Kopenhagen), ♀, Lagoa Santa, 1866

Hylonycteris underwoodi:

AMNH 178904, -, Panama
 AMNH 189688, -, Mexico
 AMNH 238199, ♀, Panama
 AMNH 256826, ♀, Belize
 BMNH 3.2.1.3, -, Taibaca, Costa Rica, leg. C.F. Underwood
 BMNH 3.2.1.4, -, Taibaca, Costa Rica, leg. C.F. Underwood
 BMNH 3.2.1.5 (**Type**), -, Rancho Redondo, Costa Rica, leg. C.F. Underwood

Scleronycteris ega:

BMNH 7.1.1.671 (**Type**), -, Ega, Amazonas, Brazil, James Collection Bates

Choeroniscus godmani:

AMNH 131765, ♂, San José, Costa Rica, leg. C.F. Underwood, 18.6.1938
 AMNH 172778, -, Tapanatepec, Oaxaca, Mexico, leg. A. Johnson, 27.1.1954
 AMNH 172779, ♂, Tapanatepec, Oaxaca, Mexico, leg. A. Johnson, 27.1.1954
 BMNH 79.12.24.1, ♂, Guatemala, leg. D. Godman
 SMF 43028, ♂, Finca el Buque, Villavicencio, Dept. Meta, Colombia, leg. E. Thiery, 15.5.1979
 SMF 41990, ♂, Finca el Buque, Villavicencio, Dept. Meta, Colombia, leg. H. Stephan, 29.6.1991
 USNM 385917, ♀, Merida, 59km SE El Dorado, Venezuela, 9.6.1966, SUP
 USNM 385919, ♀, Bolivar, 59km SE El Dorado, Venezuela, 13.6.1966, SUP
 USNM 385920, ♀, Merida, 59km SE El Dorado, Venezuela, June 1966, SUP

Choeroniscus minor (= *C. inca*, = *C. intermedius*):

AMNH 67625, ♂, Los Pozos, Ecuador
 AMNH 140471, ♀, Kamakusa, British Guayana, leg. H. Lang, 5.2.1923
 AMNH 142901, -, British Guayana
 AMNH 230285, ♀, San Pablo (900m), Prov. Oxpampa, Dept. Pasco, Peru, leg. J.C. Kelly, 12.7.1964
 BMNH 53.3.19, -, Rio Cupari, Bates Collection
 BMNH 69.1275A, ♀, Araenga, Para, Brazil, leg. R. Lainson, 18.10.1969
 BMNH 69.1275B, ♀, Araenga, Para, Brazil, leg. R. Lainson, 17.10.1969
 MEPN 7551, ♀, Plan Piloto, via Quinde, Esmeraldas, Ecuador, leg. L. Albuja, 3.5.1975

JK 189, -, Peru, leg. J. Koepke

JK 2, -, Peru, leg. J. Koepke

SMF 54044, ♀, Manau, Brazil, leg. U. Schnitzler, 2.1977

SMF 69883, ♂, Camp Caiman, Montagnes de Kourou, Fr.-Guayana, leg. D. Kock & H. Stephan, 10.1985

SMF 69802, ♀, Camp Caiman, Montagnes de Kourou, Fr.-Guayana, leg. D. Kock & H. Stephan, 10.1985

ZIM (OS) 1982, -, Rio Cuyabeno, Ecuador, leg. E. Patzelt, 1982

USNM 361573, ♀, Belem, Fazenda Velho, Para, Brazil, leg. C.O. Handley, 1965

USNM 361574, ♀, Belem, Fazenda Velho, Para, Brazil, leg. C.O. Handley, 1965

USNM 361575, ♂, Belem, Fazenda Velho, Para, Brazil, leg. C.O. Handley, 1965

Choeroniscus periosus:

AMNH 217038, ♀, Colombia

Choeronycteris mexicana:

AMNH 212358, ♂, Cerro de San Felipe, Oaxaca, Mexico, leg. T. MacDougall, (2815), 1965

AMNH 212359, ♂, Cerro de San Felipe, Oaxaca, Mexico, leg. T. MacDougall, 1965

AMNH 212360, ♀, Cerro de San Felipe, Oaxaca, Mexico, leg. T. MacDougall, 1965 (7/12)

AMNH 212361, ♂, Cerro de San Felipe, Oaxaca, Mexico, leg. T. MacDougall, (2818), 1965

AMNH 212362, ♀, Cerro de San Felipe, Oaxaca, Mexico, leg. T. MacDougall, (2819), 1965

AMNH 212365, ♀, Cerro de San Felipe, Oaxaca, Mexico, leg. T. MacDougall, (2822), 1965

BMNH 60.449, ♀, Sonora (8mls NE Imuris), Exchange with Univ. Kansas

BMNH 75.2.27.60, -, Duenas, Guatemala

BMNH 27.11.1935, ♀, Los Masos, Jalisco, Mexico, Exchange with Genua Museum

MHNG 1177.16, no data

ZFMK 77.652, -, Sierra Mixteca, Mexico

USNM 50800, ♂, Querendaro, Michoacan, Mexico, 5.8.1892

USNM 50801, ♀, Querendaro, Mexico, 5.8.1892

USNM 50802, ♀, Querendaro, Michoacan, Mexico, 5.8.1892

USNM 50803, ♂, Querendaro, Michoacan, Mexico

USNM 50804, ♀, Querendaro, Michoacan, Mexico

Choeronycteris (=Musonycteris) harrisoni:

AMNH 235179, ♂, Mexico

BMNH 61.1612, ♂, Colima, Mexico, ded. Univ of Arizona

SMF 22500, ♂, Pueblo Juarez, Colima, Mexico, leg. A.L. Gardner, 1.4.1960

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